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# THE CONDOR

#### JOURNAL OF THE COOPER ORNITHOLOGICAL SOCIETY

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Edited by Alden H. Miller

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### THE CONDOR

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NUMBER 1

#### NESTING BEHAVIOR OF THE CLARK NUTCRACKER

By L. RICHARD MEWALDT

In March and April of 1947, near Missoula, Montana, detailed observations were made of the nesting activities of a pair of Clark Nutcrackers, *Nucifraga columbiana*. A few additional data were obtained from three other nests in 1947 and one nest in 1948, all near Missoula, and from one nest in 1952 in Stevens County, Washington. Since plans to supplement the 1947 findings with further detailed observations have not materialized, it seems wise to present the material on hand at this time.

Bendire (1889) first found nesting Clark Nutcrackers in 1876 in the Blue Mountains of Oregon. His account and those of Bradbury (1917) and of Dixon (1934) include observations on nesting behavior. Briefer accounts of nesting include those of Pyfer (1897), Parker (1900), Johnson (1900 and 1902), Silloway (1903), Saunders (1910), Skinner (1916), Racey (1926), Bee and Hutchings (1942), Mewaldt (1948 and 1954), and LaFave (1954).

Nesting activities of the Thick-billed Nutcracker, Nucifraga caryocatactes caryocatactes of northeastern and eastern Europe are but little better known than those of the Clark Nutcracker. Among the more important accounts on the European species are those of Vogel (1873), Bartels and Bartels (1929), and Steinfatt (1944). A significant study of the Thick-billed Nutcracker is being made in Sweden by P. O. Swanberg (1951 and personal communication). Except for two accounts (Formosof, 1933, and Grote, 1947), information on the Slender-billed Nutcracker, Nucifraga caryocatactes macrorhynchos of the USSR is generally less available. Other subspecies of Nucifraga caryocatactes, widely distributed in Asia, are less well known.

#### ACKNOWLEDGEMENTS

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For material assistance and counsel I am indebted to Dr. Ludvig G. Browman, Dr. Royal Bruce Brunson, Dr. Gordon B. Castle, Dr. Clinton H. Conaway, Dr. Donald S. Farner, Mr. William B. Hebard, Dr. Ernst Mayr, and Dr. George C. Ruhle. I am especially grateful to Dr. Philip L. Wright for his encouragement, guidance, and help while I was a graduate student at Montana State University from 1946 to 1948. Mrs. Frances Lee Mewaldt assisted me in the field and in the laboratory.

#### METHODS

The nesting study is one portion of a life history study of the Clark Nutcracker conducted from October 1946 to May 1948 and continued on a more limited basis through 1952. Most of the observations reported here were made in western Montana, on Marshall Mountain near Missoula in Missoula County and in the Bitterroot Mountains of Ravalli County. The nests were situated between 4000 and 5000 feet in elevation, or from 500 to 1500 feet above the valley floors of the Missoula and Bitterroot

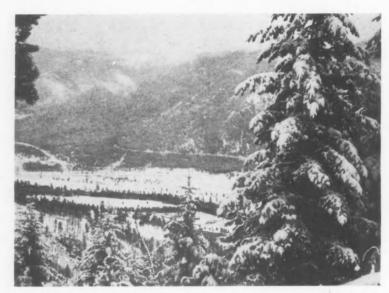


Fig. 1. Valley of the Clark's Fork (Missoula) River a few miles east of Missoula, Montana. Photograph taken on March 11, 1947, from vicinity of nest 1 of Clark Nutcracker.

rivers. Although predominately forested with relatively open stands of yellow pines (*Pinus ponderosa*) at these elevations, slopes less subject to desiccation are occupied by Douglas firs (*Pseudotsuga taxifolia*). A few of the later observations were made in eastern Washington and northern Idaho. Some reference will be made to information obtained from 439 specimens collected for studies on reproduction and molt. The results of these later studies will appear in separate papers.

Nests are numbered in the order in which they were found begining on March 11, 1947. Early during the period of incubation an elevated blind was constructed about twelve feet from nest 1, where most of the observations were made. The distance from the observation port of the blind to the nest was gradually reduced to six feet. At this distance, the nutcrackers apparently completely ignored the occupied blind as well as shutter noises of still and motion picture cameras. Observations on the activities of the nutcrackers and other vertebrates at and in the vicinity of the nest were recorded continuously during the hours the blind was occupied. Air temperature and other weather data were recorded at least hourly.

On the first day that observations were made from the blind, April 1, one of the adults was captured by hand on the nest and banded with an aluminum band. After the young left the nest this adult was collected and found to be the female of the pair. Especially because of this band, no difficulty was encountered in distinguishing between the individual adult birds of nest 1. Eggs in nests 1 and 2 were numbered with ink as laid, and the young in both nests were ink-marked to permit individual identification. At about ten days of age, the nestlings were banded. Daily or bidaily weights to the nearest tenth of a gram were obtained with a laboratory balance after detectable fecal sacs had been eliminated.

#### VOICE

The Clark Nutcracker uses a considerable variety of calls which vary with the stimulus, season of the year, age, and perhaps sex. In the spring of 1949, recordings were made of many of the calls of two adults kept in an outdoor aviary at Pullman, Washington. These birds had been live trapped in the Cascade Mountains of southern Oregon a few months earlier. I sent one of these recordings to P. O. Swanberg of Skara, Sweden. He comments in a personal communication that all of the calls except one are similar to those of the Thick-billed Nutcracker of Sweden and that the variety of notes is suggestive of those used by the European bird at morning gatherings in late summer and early spring (see Swanberg, 1951).

For use in the discussions of behavior, names have been assigned to nine of the types of calls most commonly heard.

1. Regular call. Described variously as khaaa or khraa (Peterson, 1941), chaar, char-r-r, chur-r-r, kra-a-a, or kar-r-r-rcack (Bent, 1946), and kar'r'r'r (Bailey, 1918), this harsh call is the one most frequently uttered by both sexes and is heard during all months of the year. Under favorable conditions it may be heard at distances of more than a mile. Usually given in series of three's, it may also be given only once, or many times in succession when the bird is excited. When used by juvenal birds, there is a squalling quality to the call.

2. Musical call. Similar in some respects to the foregoing, this call is comparatively liquid and soft. Its carrying quality is not great. I have heard it most often, but by no means exclusively, during the late winter and spring months when both sexes use it during the pre-nesting and nesting periods.

3. Shrill call. This high pitched and penetrating screech, described by Dawson (1923) as meack, or mearrk, is given by both males and females. Generally given during apparent excitement, this call may be heard during all months of the year. A metallic variation of the shrill call may be designated the trumpet call.

4. Squalling call. This call uttered during periods of apparent excitement is best described as a squalling prolongation of the regular call. It may be uttered by either sex of all ages during any month.

5. Bullfrog call. Heard only from December to June, this peculiar call, a comparatively slow rattle, sounding much like the "croaking" (see LaFave, 1954) of a frog, is given by both sexes of adults and by at least first-year females.

6. Crackle and whistle call. The alternating crackles and wheezing whistles are scarcely audible at 75 feet. The bird uttering this call does considerable bowing and neck stretching in contrast to the more or less conventional posture maintained when other calls are given. Heard on several occasions by birds of both sexes during only March and April, it would seem that this call is associated with the nesting period.

7. Hunger call. Much like the hunger calls of young crows (Corvus brachyrhynchos), these squalling notes, similar in quality to the squalling call, are given by juvenal birds during the spring and summer months (as late as August 10 in 1947) when they "beg" for food. Female nutcrackers occasionally use this call during courtship.

8. Conversational squalling. During the first few days after the young of nest 1 had hatched, the adults, when both were present at the nest, engaged in subdued musical squalling, similar in quality to the *musical call*.

9. Nestling calls. Within 24 hours after hatching, the young of nest 1 began peeping. This continued almost constantly during at least the daylight hours of the first week. These peeps, heard at a rate of about 35 per minute from two 24-hour nestlings, were scarcely audible ten feet from the nest. This peeping continued during actual brooding and increased in tempo when feeding was in progress. After about one week the peeping

was gradually replaced by squealing and could be heard only during feedings. The pitch of this squealing became lower and finally became the squalling characteristic of the older nestling when being fed, or when being disturbed.

Generally speaking, the Clark Nutcracker is a noisy bird most easily located by its calls. In areas where the birds are present in some numbers, their calls may usually be

heard throughout the daylight hours.

Although nutcrackers feeding on the ground are usually silent, they mount nearby trees or rocks at intervals and utter the regular, shrill, musical, or bullfrog calls. These frequent calls probably serve to preserve contact when two or more birds are moving in company while foraging. When engaged in fly-catching, nutcrackers are usually silent. Tree-foraging nutcrackers are usually noisy. Paired adults apparently use the musical call, as a means of communication. From October, 1947, through February, 1948, most birds observed were paired. These pairs were frequently discovered by their use of the musical call. On occasions when one of such a pair was collected, the other bird would leave as the shot was fired, but would frequently return to the area one or two minutes later uttering the musical call. In each such instance, when both were collected, one was later sexed as a male and the other a female. When harassing perched hawks or owls, the regular call is generally used while the nutcracker is 15 or more feet distant from the raptor, but as the nutcracker approaches more closely, it uses the squalling call. During aerial pursuits of flying hawks or eagles, I have heard nutcrackers uttering the regular, squalling, shrill, and bullfrog calls.

#### COURTSHIP

There is evidence that once paired, Thick-billed Nutcrackers of Europe remain paired for the life of both individuals. Steinfatt (1944) states that outside of the breeding season he has often seen pairs of these nutcrackers together and that it is increasingly evident that the species is a permanent resident of the Rominte Heide of northeast Poland (formerly East Prussia) and that individuals remain permanently paired as, for example, do magpies (*Pica*) and ravens (*Corvus*). Linsdale (1937) indicates that among American Magpies, mated pairs tend to remain together as long as both birds live. Swanberg (1951) finds that Thick-billed Nutcrackers "pair for life" (p. 551). During the fall and winter of 1947–48, when only Clark Nutcrackers two years old or older were present in the western Montana study areas, most nutcrackers were encountered in two's. In October and November of 1947, isolated pairs were collected on four occasions and in each instance, one was a male and the other a female. The extent to which the pair's bond is preserved by attachment of each individual to the same territory is difficult to ascertain.

Courtship is generally considered to include those activities which aid directly in bringing together males and females for reproduction of the species. In species such as the Clark Nutcracker, in which birds once mated tend to remain paired year after year, courtship or courtship-like activities may facilitate the synchronization of the male and female sexual cycles. How such activities may differ from those leading to the formation of new pairs is unknown to me. The histories of the individuals in the accounts which follow are unknown, except that all participants were probably two years old or older. Because of the variation in courtship behavior observed, none of these accounts can be considered typical.

On the morning of March 6, 1947, observations were made at about 5200 feet on a ridge near the junction of the Missoula and Bitterroot rivers. North-facing slopes were covered with a dense growth of Douglas firs, south-facing slopes with open stands of yellow pines, and the crests of the main and feeder ridges with mixed stands of both species. There were from three inches to three feet of fresh and old snow on the ground, the sky was clear and the air temperature about 25°F. At 10:10 a.m., I heard and then saw three nutcrackers on the pine slope. At intervals one bird started in rapid flight and another followed an instant later. Staying about 50 feet above the ground, they flew about 200 yards up a feeder ridge and returned to the same or an adjacent tree. From 10:20 to 10:30 a.m., eight such flights were made. The third bird did not participate and disappeared from the area about 10:25. The two birds did not return from the ninth flight. When I found them on the main ridge at 10:35, they also saw me and took up positions on either side of me giving the regular call occasionally. At 10:40 another pair of nutcrackers appeared from up the ridge, the larger (probably a male) carrying a twig in its beak. Nine times between 10:40 and 10:50, the smaller bird, loudly uttering the regular call, proceeded in rapid flight about 150 yards over the Douglas fir covered slope and each time returned to the same tree. The larger nutcracker, with twig in beak, followed in equally rapid flight, but without calls audible to me. Although the first-mentioned pair remained silent, one of the birds (the same each time) twice joined in the last part of a flight. At 10:50 the first pair proceeded up the ridge and the second pair down the ridge. Upon following the second pair, I found the larger bird carrying a twig when nearly a half mile down the ridge. Three additional flights, similar to those last described, were observed before this pair also proceeded up the ridge toward higher country.

On February 25, 1947, at 4400 feet on the southwest facing slope of Mitouer Ridge on Marshall Mountain, in the same area where nests 1, 2, and 3 were later found, there were snow-free patches of ground under some of the larger pines. The air temperature was 27°F, and the sky was partly cloudy. At 1:45 p.m. a nutcracker with a twig in its beak constantly uttered the musical call as it flew from tree to tree and then to the snow-free ground below a pine where another nutcracker was standing. After a few seconds it flew to a large Douglas fir, broke off eight or ten dead twigs in fast succession, dropped each in turn, and then returned to the bird on the ground without a twig. During the next 25 minutes the two birds in company flew among large trees, clumps of young trees, and the ground, both almost constantly uttering the musical call. One of the birds kept a dead twig in its beak most of the time. At 2:20 one bird suddenly gave the shrill call (there was no indication that my presence had been detected), and they flew together up slope something over 200 yards.

Between 4:15 and 4:45 p.m. on April 8, 1947, the sky was overcast and occasional light rain fell. About 400 yards up Mitouer Ridge from nest 1, two adult nutcrackers were under continuous observation. Constantly squalling, the smaller of the two followed the larger from tree to tree and occasionally to the ground. Finally in the dead top of m pine, the larger bird approached and appeared to feed the smaller crouching bird, by placing its beak well into the smaller bird's mouth several times. The smaller bird then stopped its squalling and they moved together from tree to tree out of the area.

At 9:45 a.m. on April 17, 1947, while I was in the blind at nest 1, a performance similar to that noted on April 8 was observed to include five minutes of begging and then an apparent feeding. This occurred partly in the territory around nest 1. Both participants were adults, or possibly first-year birds. The male of nest 1 flew at and drove the two birds down slope from nest 1 just after the apparent feeding. On April 24, the adults of nest 1 were observed in this same begging-and-feeding routine within their territory five days before the young left the nest. I was unable to distinguish the roles taken by each bird.

At nest 1 the brooding adult was observed to crouch, droop its wings, open its beak, and usually squall on about half the occasions when its mate arrived to feed the young. These actions usually took place on the edge of the nest. The female, on one occasion, actually fed the male at the nest, while in all other instances the begging tactics were apparently ignored. No such behavior was observed during the period of incubation at nest 1.

#### TERRITORY

The Clark Nutcrackers nesting on Mitouer Ridge appeared to have well defined territories. Although I became familiar with territorial limits around nest 1 only, some defense of areas around nests 2 and 3 was observed. It is apparent that there are important differences between the observed territorial behavior of the Clark Nutcrackers nesting on Mitouer Ridge and the territorial behavior of the Thick-billed Nutcrackers nesting at Billingen in central Sweden (Swanberg, 1951). Swanberg writes (p. 550), "In spite of intensive studies of nutcrackers for many years, I have never observed any

true territorial fights or any consistent defense of the territory against intruders by means of sounds or posturing. Nevertheless, each pair obviously has its defined territory. As example, my nutcracker pair A are proved to have held the same territory for at least ten years. During this time I have found fourteen nests of A in it; but although A has always been surrounded by other pairs, other nutcrackers have never made any



Fig. 2. Nest of Clark Nutcracker situated 15 feet up in 25-foot Douglas fir indicated by arrow. Photograph taken March 11, as nest was being built.

attempt to nest in the same area. Broadly speaking, the areas are used only by their holders, but it is not unusual for other nutcrackers to trespass and rest in them without being attacked, and sometimes they may even pay friendly visits to each other, as during the ceremonial gatherings, which take place in the morning immediately before or during nest building." In contrast, the Clark Nutcrackers on Mitouer Ridge did defend their nest territories against other nutcrackers by sounds and pursuit. Trespassing nutcrackers were attacked and driven off the territory if the male was present and not incubating or brooding.

Because territorial conflicts at nest 1 were very similar, I will describe in some detail one from the 14th day of incubation. On April 1 at 9:38 a.m. I had been in the blind for 98 minutes. The female had been on the nest continuously during this time. Two nutcrackers entered the territory and perched in the upper portion of a dead topped pine about 50 feet east of the nest tree. As they settled, the male of nest 1 flew from one of his perches northwest of the nest to a high stump 40 feet east of the nest tree and a moment later flew up at one of the two trespassers. The attacker and the attacked squalled as they fluttered together toward the ground. Before reaching the ground they separated, each taking low perches about 40 feet apart on opposite sides of the nest tree. Almost immediately, the male of nest 1 uttered the shrill call and flew at the same bird. The two birds, alternately hopping and flying along the ground, and constantly squalling and fighting, passed below the blind and nest to a point about 30 feet east of the nest where they both took wing and disappeared from view over the edge of the ridge. The second trespasser had in the meantime disappeared. About a minute later the male of nest 1 returned to one of his east boundary perches and gave the regular call about ten

times. Throughout these proceedings, which took about four minutes, the female on nest 1 maintained an "alert" attitude.

In most cases, the male of nest 1 was definitely known to be the defender of the territary, whereas the female was not observed to make any such defense. The female was not easily excited; while incubating or brooding, she did not react to other nutcrackers on the territory unless her mate was actively in defense of territory and using his voice. The male, however, was constantly "alert" while incubating and reacted immediately to many more outside influences than did his mate; he turned in the direction of trespassing nutcrackers when they called, but did not leave the nest while he was incubating or brooding. In the case of the pair of nest 2, both birds pursued and drove off a nutcracker trespassing on their territory before they had successfully built a nest.

The territory surrounding nest 1 was about 2.1 acres in area as enclosed within seven boundary perches. These perches varied in ground distance, 33 to 89 yards from the nest tree and in most cases were in the only large trees (75 or more feet tall) between 25 and 100 yards of the nest tree in a given direction. Toward the northwest, where there were several apparently suitable perches, the ground distances to boundary perches were found to be 52 and 63 yards. Nest 2 was situated 415 yards southeast of nest 1 while nest 3 was in a tree only 144 yards northwest of nest 1. Other nutcrackers were frequently observed to pass and occasionally stop for several minutes between the territories of nests 1 and 2 without being attacked. The territory around nest 1 was less than one-tenth the size of the "territories" described by Swanberg (1951) for the Thickbilled Nutcracker in Sweden. It should be noted that Swanberg's nutcrackers used their territories for the storage of hazel-nuts (Corylus avellana) which they harvested and stored during the fall months for use during the winter months and during the following spring for both themselves and their young. Although I have since 1947 seen Clark Nutcrackers transporting and storing pine nuts (from Pinus ponderosa), I have no evidence to indicate that the birds nesting on Mitouer Ridge in 1947 used any such stores. The birds left their territory and apparently traveled some distance to favorable foraging areas to obtain pine nuts still available on trees and in litter on the ground. Dixon (1934) in California found that a large share of the food for the nestlings was secured from an area 400 feet lower in elevation than the nests and at least one-half mile distant

During the periods when the incubating or brooding bird was alone on the territory, no defense was made. It appeared that the female was gone from the nest only long enough to feed. This left the male a considerable amount of time when he was observed to perch silently on the northwest (high) edge of his territory. Although precise data were not obtained, this male was "on guard" approximately one-half the daylight hours.

Nest materials for nests 1 and 2 were obtained, at least in part, from areas outside of the territories known to be defended during incubation and brooding. Many of the Douglas fir twigs used in nest 1 came from two partially dead trees approximately 40 yards beyond territorial limits, The pair building nest 2 crossed a gulch 400 feet deep to secure twigs from a slope more than 600 yards from the nest tree.

Other species of passerine birds were tolerated within the territorial limits of nest 1 without known exception. Species observed within 30 yards of the nest were Cyanocitta stelleri, Pica pica, Parus atricapillus, Parus gambeli, Sitta carolinensis, Sitta canadensis, Sitta pygmaea, Turdus migratorius, Sialia currucoides, Regulus satrapa, Carpodacus cassinii, Loxia curvirostra, and Junco oreganus. A male junco, whose territory overlapped the territory around nest 1, was apparently ignored by the incubating female nutcracker on two occasions when the junco sang from the top of the blind less than eight feet from nest 1.

Hairy Woodpeckers (Dendrocopos villosus) and Red-shafted Flickers (Colaptes cafer) were frequently in or near the territory around nest 1. Both adult nutcrackers, while incubating or brooding, assumed an "alert" attitude when a flicker would utter its kee-yer call within 50 or 75 yards of the nest, but no pursuit of a flicker was seen. On one occasion a Pygmy Owl (Glaucidium gnoma) called for about two minutes from a tree about 25 yards from nest 1. The incubating female appeared disturbed and turned her head in the direction of the sound, turning back to her former position only when the owl had stopped calling. The presence of a Red-tailed Hawk (Buteo jamaicensis) approximately 300 yards from nest 1 was sufficient in one instance to cause the male to leave his territory and attack in company with the nutcrackers of nest 2. This occurred during the period of incubation at nest 1 and the building of nest 2. The pursuing nutcrackers made repeated diving attacks toward the hawk's back causing it to swerve to the side as if to avoid being struck. On two other occasions the male of nest 1 remained on one of his territorial perches and gave the regular call in an excited manner while the two nutcrackers of nest 2 gave chase to a Red-tailed Hawk. The female, incubating on nest 1, assumed an "alert" attitude during these encounters.

No apparent notice was taken by the nutcrackers of nest 1 on two occasions when mule deer (*Odocoileus hemionus*) passed within 25 yards of the nest. The chatter of a chipmunk (*Eutamias*), which occupied a stump less than ten yards from the nest, caused both incubating nutcrackers to assume an "alert" attitude.

My presence on the territory was not protested unless I flushed one of the adults from the nest. Upon my entry to the blind, the female never flushed from the nest. The male, however, did flush while brooding, the only time he was on the nest as I entered the blind. When the young were being weighed, the female of nest 1 frequently came within ten feet of me to "protest" my presence. However, the male of nest 1, as well as both adults of nest 2, made no obvious "protest" when their young were handled.

#### NEST CONSTRUCTION

I have found six occupied nests of the Clark Nutcracker as well as several old nests. The observations reported here are based on four occupied nests studied in considerable detail in early 1947. The other nests exhibited no essential differences in placement or construction (see Mewaldt, 1954).

Nest 1.—Found on March 11, probably the second day of construction, at 4600 feet on a southeast facing slope near the crest of Mitouer Ridge near Missoula, Montana. It was 12 feet above the ground, supported by small lateral branches and flush with the east face of the main trunk of a 25-foot Douglas fir. The nest tree protruded somewhat into a small clearing which was surrounded on all sides, except on the east, by firs similar in size to the nest tree.

Nest 2.—Found on April 1, the first day of construction, at 4200 feet on the south-facing slope of Mitouer Ridge about 415 yards south-southeast of nest 1. It was six feet above the ground near the end of a heavily foliaged branch of an isolated 25-foot Douglas fir.

Nest 3.—Found on April 15, the first day of construction, at 4700 feet on the crest of Mitouer Ridge about 145 yards northwest of nest 1. It was placed in the heavily foliaged terminal portion of a southwest lateral branch about 80 feet above the ground in a 125-foot yellow pine.

Nest 4.—Found on April 27, when the one remaining young nutcracker was about 20 days old, the nest was at 4300 feet on a southeast-facing slope in the Bitterroot Mountains near Florence, Montana. It was placed four feet out on a south lateral branch and about 25 feet above the ground in a 50-foot yellow pine.

All nests seen were similar in composition and structure, except that bowls of old nests were somewhat broader and shallower as a result of occupancy. Nests 1 and 2 were measured early in the incubation period and later collected for examination of their component parts. Outside diameters of nests 1 and 2 varied from 11 to 13 inches. Nest 1

was seven inches high and nest 2 was six inches high. The nest bowls were about four inches in diameter and about three inches deep. The floor and outer walls of nest 1 contained 247 dead Douglas fir twigs and eight twigs from deciduous shrubs making up a dry weight (255 twigs) of 256 grams. The outer wall and thinner base of nest 2 contained 193 Douglas fir twigs with a dry weight of 144 grams. Diameters of twigs varied from one-sixteenth to three-sixteenths of an inch. Lengths of twigs were up to 12 inches with eight- to nine-inch twigs being most common. Twigs in nest 1 were generally larger than those in nest 2. The outer portion of each bowl was composed of rotten wood pulp and the inner lining of dried grass and fine strips of the inner bark from Douglas firs. In the base of each nest, between the wood pulp and the grass lining, there was a layer of mineral soil about one-half inch thick. This mineral soil was carried to the nests in damp pellets between one-quarter and three-eighths of an inch in diameter. Eight such pellets were found on the incomplete floor of nest 1 on March 15.

Except for the layer of mineral soil and differences in source plants for nest material, these nests compare well with nests of the Clark Nutcracker described by Bendire (1895) and Dixon (1934), and with those of the Thick-billed Nutcracker of Europe described by Steinfatt (1944). However, Bartels and Bartels (1929) detected in the floor of a nest of the latter species a layer of "arable" soil which was in the same relative position as the soil layer in nests 1 and 2. No evidence of the "landing platform" described by Dixon (p. 233) was found associated with any of my nests.

Although both members of the pairs building nests 1, 2, and 3 shared about equally the collection of nest material, the females accomplished most of the actual construction. While a female adjusted and arranged the freshly collected material, the male would usually fly to a nearby lookout perch where he would remain for 30 to 90 seconds before making another trip for material. This sex distinction (at nests 1 and 3 only) was based on my familiarity with the individual birds of nest 1 and on an observed size difference between the birds of nest 3. Weights of the adults of nest 3 eight days after the nest-building was begun were 122 grams for the female and 151 grams for the male.

Nest 1 was found during a heavy snowfall at 10:10 a.m. on March 11. There were four to six inches of fresh snow on the ground in addition to old snow up to three feet deep within a few feet of the nest tree. One of the birds carrying a twig into the nest tree revealed the presence of the nest. During 85 minutes of nest building observation time, of which 40 were on March 11 (10:20 to 11:00 a.m., temperature 32°F.) and 45 on March 12 (9:35 to 10:20 a.m., 34°F.), 44 individual trips to the nest were made with material. Each bird arrived at the nest tree with a twig about every fourth minute. Five times (ten trips) the birds flew together from the material gathering area (about 100 yards from the nest). Entrances into and exits from the nest tree were made in nearly every possible direction by both nutcrackers. The musical call was occasionally uttered by both birds especially while they were carrying twigs in their beaks. The male gave the regular call three to six times on each of four times he mounted a lookout perch between trips. The bullfrog call and the shrill call were uttered by both birds on several occasions, especially in the vicinity of the trees where the twigs were gathered. Once upon my approach to the nest, the female repeated the crackle and whistle call several times before retreating into the Douglas fir thicket adjacent to the nest tree. Snow fell continuously during both periods of observation.

Data were gathered for 75 minutes during the first hours of construction of nest 3 during the early afternoon of April 15. The weather was mostly clear with the air temperature about 50°F. Some 51 trips with nest material were observed. In 20 cases (40 trips) the two birds flew together from the material trees. Each bird made a trip to the nest with material about once each three minutes.

Nest 2 was found on April 1 at 7:25 a.m. (weather mostly cloudy and temperature 30°F.) when each of the two nutcrackers was seen to enter the nest tree with a twig. Whereas material for nests 1 and 3 was obtained within 125 yards of the nests, at least some of the material used in nest 2 was carried a distance of more than 600 yards. The two birds stayed together from the time they left the nest area until they returned to the nest tree on each of the six trips observed.

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Table 1
Initial Stages of Nesting in 1947

Nest	Found	Begun	Completed	First egg	Probable construction time
1	March 11	March 101	March 17	March 19	8 days
2	April 1	April 1	April 5	April 7	5 days
3	April 15	April 15	April 19 <sup>2</sup>	April 212	5 days <sup>2</sup>

<sup>1</sup> An estimate based on the rates of construction of nests 2 and 3.
<sup>2</sup> Female contained three freshly ruptured ovarian follicles when collected at 4:50 p.m. on April 23.

It is highly probable that nests 2 and 3 were found on the day construction began, while nest 1 was likely found on the second day of its construction. Nest 2 consisted of about 20 twigs at 7:25 a.m. on April 1, and was already a well shaped nest at 6:20 that evening. Nest 3 was so thin at 2:05 p.m. on April 15 that the sky could be seen through its center from about 80 feet below. Nest 1 was less advanced at 11 a.m. on March 11 than nest 2 at 6:20 p.m. on its first day of construction (see table 1).

Work on nests 1 and 2 continued until, but apparently not including, the day before the first egg was laid. Because of the inaccessibility of nest 3, the incubating female was collected on the eighth day after the nest was begun. At autopsy she contained three freshly ruptured follicles in her ovary, there was no egg in the oviduct, and all other follicles were relatively small. Efforts to recover the nest were not successful.

#### AN INSTANCE OF ABERRANT NEST-BUILDING BEHAVIOR

At 9:10 a.m. on March 24, 1947, a pair of Clark Nutcrackers, thought to be the same pair which on April 1 began construction on nest 2, were seen carrying twigs to a pine about 140 yards north-northeast of their later successful nest. The twigs were placed on a comparatively open fork of a lateral branch about 10 feet above the ground. During the following week this pair spent many, if not most, of the daylight hours carrying material to this location. At no time were more than 10 or 12 twigs observed at a time on this fork and usually only 2 or 3 remained in position. Although partially obscured by fresh snow, there were several hundred freshly broken twigs on the ground below this branch on March 24. Shortly after the snow had disappeared a count disclosed more than 2500 Douglas fir twigs in this pile, plus some strips of shredded bark. About 20 twigs were accumulated on a stump about 12 feet from the larger pile.

During an hour of observation (9–10 a.m.) on March 25, only the smaller bird, presumed to be the female, concerned itself with arranging the twigs. Trips for material were always made together whether to nearby trees or across Mitouer Gulch where material was later collected for nest 2. Upon their return the presumed male would leave his twig on the branch and quickly fly to a lookout perch nearby. The other bird would spend 30 to 90 seconds arranging the 10 to 12 twigs. As this bird crouched and turned about, as though shaping a nest, one or more of the twigs would fall to the pile below the tree. Once when a twig fell, the bird flew down to the pile, picked up a twig, and

returned to the fork where it again proceeded to arrange the material. On one return trip, the presumed male flew past the "nest tree" to a lookout perch, where he dropped his twig.

A nutcracker which came near the "nest tree" was pursued by both members of the pair in five or six circles about 100 yards in diameter before the intruder left the area in direct flight. The three birds were silent except about once in each circuit when they dipped near the ground and engaged in considerable fluttering, fighting, and squalling. This episode consumed about five minutes. Immediately after the third bird disappeared up the slope toward nest 1, the pair resumed gathering twigs.



Fig. 3. Nest and eggs of Clark Nutcracker, April 13, 1948, 20 feet up in yellow pine in Bitterroot Mountains, Ravalli County, Montana.

Nice (1943) cites several instances in which various species of birds collected nesting material in excess to that needed for a given nest. In this instance, however, the female was unable to arrange the twigs so they would remain in position. It is possible that the precise site chosen did not have the requisite physical configuration to support the base of a nest. It was apparent on April 1 that little effort was wasted in the construction of the outer shell of nest 2 in the new location.

#### EGG-LAYING AND INCUBATION

Three eggs were laid in nest 1 and in nest 2, and probably also in nest 3. Nest 5, found on April 13, 1948, in the Bitterroot Mountains near Stevensville, Ravalli County, Montana, contained three eggs in an advanced stage of incubation. Nest 4 held one nearly fledged young on April 27, 1947, and nest 6 contained three young about 14 days old when found on April 6, 1952, near TumTum, Stevens County, Washington (Me-

waldt, 1954). According to Bent (1946), the Clark Nutcracker lays usually two or three eggs, but often four and occasionally as many as five or even six. Of six nests of the Thick-billed Nutcracker of Europe observed by Vogel (1873), five contained four eggs each and one contained three eggs.

Although the eggs were almost certainly covered by the adults from the time that the first egg was laid, actual incubation probably did not begin until the last egg was laid (see Swanberg, 1951). The mean temperature for March (1892–1946) at Missoula, about 1500 feet lower in elevation than nest 1, was about 2°C., and the mean minimum about -4°C. In order not to be frozen, the eggs must not only be covered but must also receive some warmth from the bird on the nest during the pre-incubation period.

By taking the time elapsing between the laying of the last egg and the hatching of that egg (Swanberg, 1950; Nice, 1954), the period of incubation was found to be 18 days (table 2). I have assumed that intervals of approximately 24 hours elapsed between the depositions of eggs in each of nests 1 and 2 (Miller, 1931; Nice, 1937; and Bent, 1946) and that the young probably hatched during daylight hours (Miller, 1931).

Table 2
Egg Laying and Hatching Times

Egg	Egg laid between	Probable laying time	Young hatched between Nest 1	Probable hatching time	Days from laying to hatching	Incubation period
A	1:00 p.m. March 17 2:35 p.m. March 19	a.m. March 19	4:30 p.m. April 6 <sup>1</sup> 6:55 p.m. April 7	a.m. April 7	19	18
В	10:00 a.m. March 20 8:55 a.m. March 21	a.m. March 20	6:55 p.m. April 7 <sup>2</sup>	6:55 p.m. April 7 <sup>2</sup>	19	18
С	9:25 a.m6:50 p.m. March 21	a.m. March 21	3:15 p.m. April 8 <sup>2</sup>	3:15 p.m. April 8 <sup>2</sup>	18	18
D	5:00 p.m. April 6 6:35 p.m. April 7	a.m. April 7	Nest 2 7:15 p.m. April 26 <sup>3</sup> 7:10 p.m. April 27	a.m. April 27	20	18
E	7:00 a.m5:00 p.m. April 8	a.m. April 8	do	do	19	18
F	5:00 p.m. April 8 6:45 p.m. April 9	a.m. April 9	do	do	18	18

<sup>1</sup> Egg not pipped.

At 6:55 p.m. on April 7 the sparse, but conspicuous, white down was dry on nestling A of nest 1 and its egg shell was not in the nest; nestling B was not yet free from one-half of its egg shell and the other half remained in the nest; and egg C was not yet pipped. On April 8 continuous observations were made from the blind from 7:40 a.m. to 4:05 p.m. Between 11:00 a.m. and 1:10 p.m. the female pecked egg C on several occasions. Upon flushing her at 1:10 p.m., I found the egg slightly pipped, and in line with this pip at the large end of the egg was a ring of indentations apparently pecked there by the female. She returned to the nest less than one minute after I returned to the blind. At 3:08 p.m. the female backed to the edge of the nest and pecked at egg C for four minutes, at the end of which time nestling C was free of its shell. Immediately thereafter the female proceeded to break off portions of the shell about one-eighth inch in diameter and swallow them. She then settled back to brooding at 3:16 p.m. without removing the remainder of the shell from the nest.

<sup>&</sup>lt;sup>2</sup> Hatching tim <sup>3</sup> Egg pipped.

That both male and female Clark Nutcrackers incubate the eggs and brood the young has been reported by Bendire (1895), Skinner (1916), and Dixon (1934). My findings are consistent with these reports (table 3). In this regard it is significant to note that incubating male Clark Nutcrackers have incubation patches which are fully as well developed as those of females (Mewaldt, 1952). The relative roles in incubation and brooding of the sexes of the Thick-billed Nutcracker of Europe have not as yet been clarified in publication.

During 20 hours of daylight observation in the period of incubation, the adults were attentive 99.5 per cent of the time. The female was attentive 79.5 per cent and the male 20 per cent of the 20 hours. From the time that nest 1 was completed, until the first two eggs had hatched, the adults were not seen together at the nest. Incubation changes were apparently usually made on signal by the off-nest partner as it approached the nest tree from a westerly direction. Five different calls were used by the adults in making nine incubation duty changes. The male in five approaches used the regular call twice, the musical call once, and was silent twice; the female in four approaches uttered the musical call twice, the bullfrog call once, and was silent once. On being relieved four times, the male gave the regular call twice, the shrill call once, and was silent once; the female on being relieved five times uttered the musical call twice, regular call once, bullfrog call once, and a weak whining call once. Calls were repeated from one to seven times at each exchange. At 5:21 p.m. on April 3, after 272 minutes of continuous incubation, the female gave the musical call six times in succession and was answered by the male giving the regular call four or five times from near the edge of the territory. At his answer she left the nest and the male appeared at the nest about thirty seconds later, gave the regular call twice, and settled on the nest. On three different occasions the female, after having been on the nest for more than two hours (149, 180, and 260 minutes) without relief, seemed to call to the male. On each occasion the male was in the territory and had been calling shortly before. She used the musical call each time (12, 4, and 8 times, respectively), but apparently did not get the desired response, for she remained on the nest. Twice this happened 12 minutes and once 14 minutes before she was relieved, in each instance after another exchange of calls immediately prior to the change.

The very high percentage (99.5) of attentiveness and the efficiency in exchange of incubation duties has positive survival value when freezing and near-freezing temperatures are the rule, rather than the exception, during the February to April nesting season. The apparent feeding of the incubating female Clark Nutcracker by its mate reported by Dixon (1934) and suggested similar behavior in the Thick-billed Nutcracker of Europe (Vogel, 1873; Bartels and Bartels, 1929) was not observed at nest 1.

The eggs were left uncovered 0.1 to 2.5 minutes at incubation changes. It took 2.5 minutes to complete one transfer because just as the female left the nest at the usual exchange of calls, the male became involved in a short territorial dispute with a trespassing nutcracker. On arriving at the nest the male remained more than usually "alert" for the next 3.5 minutes, although I did not hear any other nutcrackers during the first five minutes after his arrival at the nest.

When the female flushed from nest 1, she would return to and settle on the nest within one or two minutes, but the male after being flushed from the nest never returned while I was still in the vicinity. The male at nest 1 seemed to be an unusually nervous bird. At nest 2, where the individual adults were not differentiated, the nest was usually covered within two minutes after I left the nest tree. Whenever I approached an incubating or brooding bird on nest 1 or 2, it would open its beak in a wide gape (observed and photographed by Dixon, 1934) but would not take an otherwise menacing

Table 3

Summary of Attentiveness and Inattentiveness during Incubation and Brooding at Clark Nutcracker Nest 1

	April 1 14th day incubation	April 3 16th day incubation	April 8 2nd day brooding	April 11 5th day brooding	April 17 11th day brooding	April 24 18th day brooding
Time of day	8 a.m6 p.m.	7:15 a.m5:30 p.m.	7:45 a.m3:45 p.m.	6:50-11:30 a.m.	8-11 a.m.	9 a.m4 p.m.
Total time	10 hours	10 hrs. 15 min.	8 hours	4 hrs. 40 min.	3 hrs.	7 hrs.
Air temperature (°F.):						
Beginning and end	31-39	32-38	# E E E E E E E E E E E E E E E E E E E	28-39	40-52	37-40
Low and high	31-53	32-46	官用用用用发送用用用用用	28-39	40-52	37-51
Hourly mean	43	40	******	33	46	42
Wind velocity (est.)	0 to 15 m.p.h.	10 to 35 m.p.h.	0 to 10 m.p.h.	5 to 10 m.p.h.	0 to 5 m.p.h.	0 to 15 m.p.h.
Per cent sunshine	10%	40%	75%	5%	20%	30%
Snow at nest treee	0 to 18 in.	0 to 18 in.	0 to 12 in.	1 to 10 in.	0 to 8 in.	0 to 5 in.
Precipitation (% time)	20% rain and snow	15% snow	None	15% snow	None	20% rain and snow
Attentive periods, 9 &	w	9	6	10	89	9
Lengths in minutes	(118) <sup>1</sup> , 69, 161,	(30), 51, 194,	(21), 25, 43,	(3), 87, 58,	(25), 1, 2	1, 1, 1, 1, 1,
	61, (190)	55, 272, (8)	37, 158, 25,	121, (11)		1
			90, 20, (61)			
Per cent of total time	%68.66	99.19%	%96.66	99.88%	15.56%	1.19%
Inattentive periods, 9 &	4	w	-	1	3	7
Lengths in minutes	0.08, 0.25, 0.25,	150 050	0.17	0.33	40, 99, (13)	(35), 139, 22,
	1	2000	3			100000000000000000000000000000000000000
Percent of total time	0.11%	0.81%	0.04%	0.12%	84.44%	98.81%
Attentive periods, 9	33	3	25	2	3	4
Lengths in minutes	(118), 161, (190)	(30), 194, 272	(21, 43, 158, 90, (61)	87, 121	(25), 1, 2	1, 1, 1, 1
Per cent of total time	78.20%	80.65%	77.67%	74.17%	15.56%	0.83%
Attentive periods, &	2	23	4	3	None	2
Lengths in minutes	69, 61	51, 55, (8)	25, 37, 25, 20	(3), 58, (11)	None	1, 1
Per cent of total time	21.69%	18.54%	22.29%	25.71%	None	0.36%

<sup>1</sup>Periods in parentheses were not completely clocked because of the arrival or departure of the observer. Arrival and departure had no apparent effect on attentiveness or inattentiveness, as reported here.

attitude. When I remained motionless near the nest, or disappeared into the blind at nest 1, the bird would almost immediately close its beak and apparently ignore my presence. The Heinroths (1926) observed this unusual gaping behavior in the Thickbilled Nutcracker of Europe and, strangely enough, in the phylogenetically distinct Starling, *Sturnus vulgaris*.

During 965 minutes of incubation the female was observed to rise and shift position (other than to leave the nest) a total of 53 times, or about once every 18 minutes. Similarly, during 244 minutes of incubation, the male shifted position 14 times, or about once every 17 minutes. These periods of restlessness varied in duration from about five seconds to about two minutes and occurred at intervals of from 1 to 62 minutes. Restlessness did not appear to be correlated with the amount of time the bird had been incubating. During periods of restlessness, the most common activity was to rise off the eggs, back toward the edge of the nest, probe into the nest among and around the eggs, and then moving from side to side, settle back on the eggs facing in the same or a slightly different direction. It is probable that the eggs were turned and shifted in position by the bird with its beak on these occasions. It was noted that each time the relieving bird arrived at the nest its beak was glossy black, but after the first probing into the floor of the nest, it was a dusty gray, indicating that the mineral soil in the floor of the nest was dry and not a caked layer of mud. The calls of other nutcrackers, of Red-shafted Flickers, a Pygmy Owl, and a chipmunk caused the incubating bird to become more "alert," but not to shift position. During a snow squall at 7:30 a.m. on April 3, the incubating female, without rising from the nest, snapped at and seemed to catch about ten falling snow flakes.

#### BROODING AND FEEDING

Observations were made from the blind at nest 1 on the second, fifth, eleventh, and eighteenth days of the altricial period (table 3). Observations made on the ninth day were interrupted and are not included in the summaries. Attentiveness through the ninth day of brooding was nearly 100 per cent. During 664 minutes of observation on the second and fifth days, the female was attentive 75.2 per cent of the time, and the male 24.8 per cent of the time. On the eleventh and eighteenth days, the female was brooding when I arrived at the nest but did not return to the nest except for feeding after she was flushed. On the eighteenth day, when continuous observations were made from 9 a.m. to 4 p.m., neither adult was at the nest except to feed the young and clean the nest. At nest 2, to which 12 weighing visits were made in the 19 days of the altricial period, one or the other of the adults was flushed from the nest through the ninth day, but not from the tenth day onward. Steinfatt (1944) found that brooding duties were shared by the adult Thick-billed Nutcrackers in the German Alps in the early days of the altricial period.

Whereas during incubation the adults were never observed at the nest together, the adults were frequently at the nest simultaneously during about the first half of the altricial period. For the record, times when both adults were at the nest together are assigned to the bird remaining to brood. Feedings on the second and fifth days were usually signaled by the off-nest bird, which uttered the *musical call* as it approached the nest tree. Immediately after the arriving bird reached the nest, the brooding bird would move to one edge of the nest and assume a begging attitude with its wings fluttering. Ignoring its begging mate, the adult just arrived would feed one or more of the nestlings by inserting its beak well into the open mouths of one or more young at least two or three times each. The feeding bird's throat quivered as it reached the nest and feedings were made by regurgitating the shelled, partially broken-up, and well lubricated pon-

derosa pine nuts deep into the throats of the young birds. Then, with subdued squalling, both adults would probe among the young birds, where they would pick up and then swallow spilled food and freshly voided fecal sacs. One of the adults would then leave the nest and the other would settle over the young with its breast feathers well fluffed. This feeding procedure was much the same whichever bird arrived with food.

On the second day of the altricial period, the female upon arriving at nest 1, fed the begging male before she fed the young. This was the only instance observed at nest 1 wherein one adult responded to the begging of the other by feeding it. Later that same morning the male arrived at the nest, apparently ignored the begging female, and pro-



Fig. 4. Adult Clark Nutcrackers at nest 1 on April 11, the fifth day of brooding-feeding.

ceeded to feed the young. As he was feeding the nestlings, the female began working her throat muscles and also fed one of the young. She had arrived at the nest 18 minutes before, had fed the young at that time, but had not picked up any fecal sacs. This retention of food in the crop was demonstrated by the male shortly after noon the same day. Twenty minutes after he had relieved the female without feeding the young, he backed to the edge of the nest, regurgitated a quantity of shelled, partially broken-up, and well lubricated pine nuts on the edge of the nest. He then re-ate the nuts and settled back onto the nest. When the female arrived five minutes later and proceeded to feed the young, the male also fed them.

At 6:53 a.m. on the fifth day of the altricial period the male was on nest 1 when the female arrived to feed the young. While still covering the nestlings, the male squalled and fluttered his wings as though begging to be fed. When the female did not feed him, he backed to the edge of the nest, and on this singular occasion left the nest while the female was still feeding the young.

Each of the six times the female arrived at nest 1 during the observations of the

second and fifth days of the altricial period, she fed the nestlings and relieved the brooding male. During this time, the male made nine trips to the nest. On four trips he fed the young and relieved the female, on three trips he fed the young but did not relieve the female, and on two trips he relieved the female without feeding the young.

After daytime brooding ceased, the feedings followed basically the same procedure, except that the excitement apparently provoked by the presence of both birds at the nest simultaneously, was absent. Actions of the adults seemed more deliberate and they consumed less time.

Of 22 feedings observed at nest 1 during 22 hours and 40 minutes of the altricial period, 12 were made by the female and 10 by the male. Eight clocked intervals between feedings by the female were 80, 88, 92, 100, 110, 140, 145, and 183 minutes for an average of 117 minutes between feedings. Similarly, seven clocked intervals between feedings by the male were 50, 54, 75, 90, 115, 123, and 179 minutes for an average of 98 minutes. Clocked intervals between feedings by either bird varied from 10 to 140 minutes with an average of 64 minutes. Recorded intervals between feedings early and late in the altricial period did not very significantly, but a tendency to increase with nestling age is suggested. In the case of half-grown Thick-billed Nutcrackers, Steinfatt (1944), during 20 hours of observation, found that intervals between feedings varied from 17 to 110 minutes with the average interval about 45 minutes.

During the first few days, apparently being uncovered by the brooding adult was sufficient stimulus to cause the young to open their mouths for food. After daytime brooding ceased, almost any loud noise, shock, or sudden movement near the nest, seemed sufficient to induce them to open their mouths. However, at 1:23 p.m. on the eighteenth day of the altricial period, the two young remained crouched low in the nest, apparently asleep, when the female arrived on the edge of the nest. She remained perched a few seconds and then gave the *musical call*. This caused the young to raise their heads for feeding. It had been 65 minutes since the previous feeding.

Fecal sacs were usually voided by the nestlings immediately after a feeding, when the adults would promptly pick them up and either swallow them or carry them away. This prompt voiding of the fecal sacs was observed by Steinfatt (1944) in nestling Thick-billed Nutcrackers in Europe. At nest 1, during 22 hours and 40 minutes of observation during the altricial period, the female removed fecal sacs nine times (15 sacs) and the male removed them six times (10 sacs). In each of the nests observed by me, the fecal sacs were removed throughout the altricial period. They were not permitted to accumulate on the edge of the nest as is common in some passerine species such as Sturnus vulgaris and Carpodacus mexicanus.

Food for the young at nest 1 consisted almost entirely of shelled ponderosa pine nuts, although some insect material was included in feedings on April 24. The importance of vegetable food for nestling *Nucifraga* has been reported by several workers including Vogel (1873), Bendire (1895), Skinner (1916), Bradbury (1917), Steinfatt (1944), and Swanberg (1951). The general unavailability of insect food during the nesting season in the areas inhabited makes this ability to utilize vegetable food an important factor in survival. There is abundant evidence in the literature, and in my findings (unpublished data), that the incidence of nesting of Clark Nutcrackers in areas they inhabit is largely dependent on the previous year's pine-nut crop in that area. This is apparently true in the case of Old World nutcrackers, also (Lack, 1954).

#### DEVELOPMENT OF THE YOUNG

Daily or bidaily visits usually between 5 and 7 p.m. were made to each of nests 1 and 2 during the altricial period of about 20 days. Weights were taken to the closest

0.1 gram on a laboratory balance, after detectable fecal sacs had been eliminated. Each of the six nestlings was first marked with ink and later banded to assure correct identification. Because weights were taken late in the day and because four of the six subjects apparently hatched early in the day, the ages of the nestlings are given to the nearest 0.5 day (Lack and Silva, 1949; King, 1955).

A freshly hatched and unfed nestling weighed 7.1 grams, whereas three nestlings at 0.5 day of age weighed 7.5, 8.0, and 8.2 grams. The mean weight of the four surviving young was 95.3 grams at an age of 16.5 days. Mean daily increments were 5.5 grams from 0.5 to 16.5 days of age. Twelve additional daily increments and decrements up to 20.5 days of age have a positive mean value of only 0.2 grams. This indicates that

weights tended to level off during the last few days in the nest.

One nestling in each brood failed to survive the altricial period. The last one to hatch in nest 1 failed to gain sufficient weight and died in the nest when 9 days old. It weighed 14.5 grams at death when its sibs weighed 50.2 and 62.3 grams. One young nutcracker in nest 2 kept pace with its sibs until 8.5 days of age. It then ceased making significant gains in weight up through 12.5 days of age and was gone from the nest on the fourteenth day. A diligent search failed to reveal its presence in the vicinity of the nest tree.

The newly hatched nutcrackers had a sparse covering of white down on their principal feather tracts. The white down became thicker until at 4.5 days dark pigmentation was first apparent in the feather papillae of the capital, dorsal, and alar tracks. On the eleventh day feathers had begun to break their sheaths and the white down was less noticeable. Feather development by 18.5 days was not yet sufficient to cover the apteria. However, when crouched in the nest in their usual position of resting, most dorsal apteria were covered, especially because the wings folded over the back.

Eyes of nestling Clark Nutcrackers began to open on the fifth day, but did not appear completely opened until the eleventh day. By their eighteenth day, the young birds spent some minutes at a time, several times during the day preening their feathers.

shaking themselves, and at times flapping their wings.

The nestlings were silent while being handled for weighing until 8.5 days of age. The squealing at this age, as well as the lower-pitched squalling of the nestlings when several days older, stimulated the adults to approach the site of the weighing more closely than before the audible responses of the young were uttered.

No coordinated attempts at escape were exhibited until one of the two nestlings of nest 1 had to be replaced in the nest a second time after weights were taken when they

were 20.5 days old.

Mouths of nestlings were observed to be bright salmon-red. At the time they left the nest they had gray eyes, gray feet, and the inside surfaces of their bills and mouths varied from pale salmon-red to white. Feathers were in growth (postnatal molt) in every tract except the capital tract. Usually primaries 1 to 9 were soft and growing, whereas primary 10 and the ten secondaries were fully grown and hard. The upper wing coverts were usually hard, with the exception of the marginal coverts, many of which were incompletely grown. The lower wing coverts were more than half grown. The rectrices were usually about one-half grown. Pitelka (1945) found young Aphelocoma coerulescens lacking lower wing coverts as late as the time of departure from the nest. In the young nutcrackers as they were leaving the nest, feathers in the central portions of most feather tracts on the body were fully grown, but those along the edges of the spinal and ventral tracts, and of the posterior portions of the humeral and femoral tracts were soft and only partially grown. The last traces of the postnatal molt appeared in the lateral portions of the dorsal region of the spinal tract.

During the postnatal molt the irises of the eyes gradually changed in color from gray to brown and the feet changed from gray to black. Black areas appeared in the white inside surfaces of the bill and mouth and gradually increased in size until well into the postjuvenal molt, when the inside of the bill and mouth of most specimens was black.

#### SUMMARY

Observations were made on the nesting activities of a pair of Clark Nutcrackers, *Nucifraga columbiana*, which nested in March and April of 1947 near Missoula, Montana. A few additional data were obtained from five other nests.

Nine calls most commonly heard are described and the circumstances incident to their use are discussed.

Considerable variation in courtship activities suggests that no simple set of behaviorisms can be cited as typical, even for the one population studied.

The territory around the most thoroughly studied nest contained at least 2.1 acres and was actively defended by the male against trespass by other nutcrackers. He used pursuit, body contact, and voice in territorial defense. At least some nest material and most of the food for the young was obtained beyond territorial limits.

Whereas both birds collected nest material, the female apparently did most of the actual building. Nest placement was highly variable, nests being found from 6 to 80 feet from the ground, in either *Pseudotsuga taxifolia* or *Pinus ponderosa*, the only suitable species of trees in the areas most intensively studied during the nesting season. Construction time on two nests was five days each and on one nest was eight days. An instance of aberrant nest building behavior is described.

The male Clark Nutcracker develops an incubation patch. During 20 daylight hours, a male was clocked incubating 20 per cent of the time. Better than 99 per cent attentiveness assured adequate protection to the eggs even during sub-freezing weather. The period of incubation was found to be 18 days.

Attentiveness of the adults was essentially 100 per cent during the first nine days of the altricial period. Thereafter the young were not covered during most of the day-light hours. The male was attentive 25 per cent of the time during 11 hours of observation on the second and fifth days of the altricial period. Intervals between feedings by either adult varied from 10 to 140 minutes with an average of 64 minutes.

Four nestlings in two nests gained an average of 5.5 grams per day during the first 16.5 days of about 20 days in the nest. Food for the nestlings consisted almost entirely of shelled nuts from *Pinus ponderosa* supplemented by some insects late in the altricial period.

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## POPULATION STRUCTURE IN SALT MARSH SONG SPARROWS PART I. ENVIRONMENT AND ANNUAL CYCLE

#### By RICHARD F. JOHNSTON

The Song Sparrows (*Melospiza melodia*) that live on the salt marshes of San Francisco Bay, California, have attracted the attention of students of birds for the past sixty years. The principal reason for this has been their morphological distinctness from all other Song Sparrows, including those that live in areas close to the salt marshes. Such a pattern of differentiation and distribution has always raised the problem of how the salt-marsh populations maintain themselves as distinct entities. The study reported now is a continuation of previous work on salt-marsh Song Sparrows; the questions asked were, what characteristics of salt-marsh populations influence or have some relationship to the maintenance of their morphologic and/or genetic integrity, and how do these characteristics express themselves?

Certain details bearing on these questions that are supplied in this and a succeeding paper have been interpreted in the light of the theoretical and factual framework partly supplied by such authors as Wright (1940; 1943), Mayr (1942; 1953), Miller (1947), and Marshall (1948).

The Song Sparrows studied exist partly isolated from other populations of Song Sparrows on San Pablo salt marsh, Richmond, Contra Costa County. They offered advantages not otherwise generally available to the worker in population ecology of birds: they were abundant and were situated in a discrete unit of salt marsh; they belonged to a group genetically distinctive to the extent of being accorded the taxonomic status of race (M. m. samuelis); they were non-migratory; they had been studied from a general ecological viewpoint by Marshall (loc. cit.); and they belonged to a widespread species for which Nice (1937; 1943) had compiled a definitive life history based on studies in Ohio. Thus, most of the effort in studying the birds was directed to the investigation of population structure. Since these Song Sparrows differ in certain respects from those in Ohio, a number of features of their life history that bear on population structure are included. I have not offered a comparison of these differences except where it has seemed to be particularly significant.

Generous help and counsel in the preparation of this report have been given me by Alden H. Miller, Frank A. Pitelka and Ray F. Smith; their suggestions have applied to all parts of the study. Responsibility for validity at all levels remains mine, however. The habitat photographs were taken by Joseph G. Hall. My wife, Lora Lee Johnston, assisted with preparation of manuscript. It is a pleasure to acknowledge the aid of these people.

#### METHODS

Trapping.—A variety of small bird traps, mostly of the Potter two-cell and Bailey collapsible types, constructed of hardware cloth were used in the trapping. Baits used were a variety of commercially available grains and "wild bird" seed mixtures. These were of low success in catching both juvenal and adult birds. Identical methods used in the uplands were highly successful in trapping Song Sparrows. Salt-marsh Song Sparrows do not come readily to traps baited with grain, probably due to their characteristic dietary preferences.

Nest-finding.—As a result of my inability to trap many Song Sparrows, special effort was made to find nests so that a large number of nestlings could be banded. This program was not as successful as it might have been, due primarily to the fact that the salt-marsh Song Sparrow does not have a "typical" nest site; it was therefore impossible to count on finding the nest of any specific pair. The principal method of finding nests

was to flush the incubating or sitting females from them. Rapid walking through territories was found to be best for this, for if the birds had sufficient warning of my presence, they would slip off the nest and run away over the ground surface; they would invariably never be seen in such instances (the fact that they did this was determined through observation at known nests). A few nests were found by observing the actions of the adults during the time that they were feeding nestlings and a few by prolonged search of all likely nesting sites in a given territory.

Banding.—Each bird was banded with a Fish and Wildlife Service aluminum, numbered band, plus plastic bands in a distinctive combination of colors. In the years from 1950 to 1953 I used coiled plastic strips that had to be fixed to the leg of the bird with the help of a drop of acetone base cement. In 1954–1955 I used split plastic bands of very high tensile strength. These were manufactured by the A. C. Hughes Company of Hampton Hill, England. These are especially useful on nestling birds, as they require no cementing and are affixed rapidly. A total of 287 birds was banded; of this number 241 were nestlings, 33 adults, and 13 juveniles.

Censusing.—Censuses of salt-marsh Song Sparrows may be made accurately only in the breeding season. At other time of the year the birds are, as a population, hard to see, preferring to stay in heavy cover of vegetation or in slough bottoms in the shadows. My records for all birds have gaps that represent periods of time during which it was not possible to find them. Some of the gaps are as long as one year; I have always assumed that a bird that returned but had been missing was not gone from the area but merely escaped my notice.

Marshall (1948:196) described the method of counting in the breeding season: one merely walks the length of a tidal slough and marks off on a map of that slough the occurrence of territorial males or pairs, as the case may be. One such count would be enough for most analyses, but I do not have less than two formal counts for individual sloughs in one season. Numerous additional checks of restricted parts of sloughs were made in the course of the nesting season as a result of other field activities.

#### ENVIRONMENT

Locality.—San Pablo salt marsh lies about one mile north-northwest of the center of the city of Richmond. This marsh has its front on San Pablo Bay, the northernmost part of San Francisco Bay. The bay at this point in Contra Costa County is shallow for hundreds of yards offshore; at low water about 1000 yards of mudflat is exposed off San Pablo marsh and for yet another mile the water is but four feet deep. Depths of 60 to 80 feet are reached only in the channel, cut during the last Glacial Period by the Sacramento-San Joaquin River.

San Pablo marsh is typical of relatively undisturbed San Francisco Bay salt marsh (see Marshall, 1948:205; Hinde, 1954), being composed primarily of two plant associations: a *Spartina* zone on low ground and a *Salicornia* zone on the medium to high ground. The ground surface is extensively dissected by tidal sloughs or creeks. In the younger, *Spartina* zone the sloughs are fairly straight, running at nearly right angles to the bayfront; in the *Salicornia* zone the sloughs branch and wind tortuously (fig. 1). Eventually the sloughs, becoming narrower and shallower, lose their identity on the higher marsh. The highest marsh is covered by *Salicornia* and lies flat and unbroken by any waterway. Marshall (1948:211) called San Pablo marsh a "young marsh," meaning that it was primarily a *Spartina* marsh, actively being built onto the extensive bay mudflats. This is not entirely an adequate description, for in areas to the south of where Marshall worked most of the marsh is of the *Salicornia* type, and it is in this area that the present study was conducted.

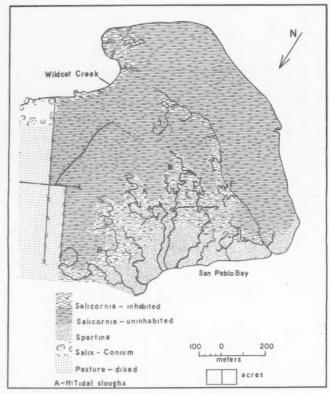


Fig. 1. Part of San Pablo salt marsh, showing vegetational associations and tidal sloughs on the study area.

The soil of the marsh is a heavy blue-black clay and on the lower marsh it is not built by deposition of plant material, but rather by the binding action of roots of Spartina. Anaerobic conditions exist in the soil of the Spartina zone a few millimeters from the surface and any disturbance of the surface demonstrates this by the immediate release of characteristic gasses, mainly  $H_2S$ , identifiable by odor. The soil is poorly drained and has a high water-holding capacity; if anywhere the surface is exposed to drying, marked shrinkage occurs with irregular surface peeling and polygonal cracking.

Vegetation.—The dominant plants of the Spartina association (fig. 2) are Spartina foliosa and, on the raised slough banks, Salicornia ambigua, Grindelia cuneifolia, and Distichlis spicata. The last three plants are properly classed with the Salicornia zone, and, indeed, penetrate the Spartina zone only on slough banks that effectively produce mid-marsh conditions because of their higher ground surface. Spartina generally is wetted by at least one tide each day. Where the marsh slopes gently into the bay and mudflat, there are found numerous young individuals of Spartina that extend the limit of the marsh.



Fig. 2. Spartina association on San Pablo marsh. The shrubby plants are Grindelia, marking the banks of tidal sloughs.

Progressing to higher ground, tidal coverage, except in March and September when tides are very low, is reduced to only about one week per month in most months. Usually a band of variable width of Distichlis borders the Spartina zone, followed abruptly by the extensive Salicornia association (figs. 3 and 4). Plants of this zone in order of decreasing abundance are Salicornia, Distichlis, Grindelia, Frankenia grandifolia, Jaumea carnosa, Triglochin striata, T. maritima, Cuscuta salina, Achillea millefolium, Cordylanthus maritima, and Atriplex patula. Spartina enters this zone in the bottoms of the tidal sloughs and also occurs in depressions in the otherwise flat marsh surface. The distribution of the two vegetation types is indicated in figure 1.

Along their lengths the sloughs have undercut banks due to tidal flow and periodically parts of the banks fall into the water ways. This builds up the level of the slough bottoms and results in further deposition of soil both on the mudflats and on the highest marsh reached by the slough. In this manner the sloughs lose their identity on the high marsh, probably at about the same rate at which the marsh advances into the bay.

Tides.—Tides in this region of North America are of the semi-diurnal type, that is, there occur two high and two low tides practically every day of the year. Due to inequality between the lengths of the lunar and solar days the tides occur each day about one hour later than on the day preceding, and it happens occasionally that only three tides occur in a solar day. There is also an inequality in the range of the tides daily due to the variation in position of the moon north or south of the equator so that usually there is a higher high tide and a lower low, the other two tides being intermediate.

The heights reached by the tides vary throughout the year. This variation is due to the coincidence or opposition of solar and lunar attractions and the distance of the moon from the earth. Tides here are highest in the periods from December to January and June to July and lowest in March and September. This brief summary of tidal con-



Fig. 3. Salicornia association on San Pablo marsh. Foreground areas are not inhabited by Song Sparrows, which live in areas marked by the Grindelia rows in the middle distance.



Fig. 4. A tidal slough in the Salicornia zone; the slough here is 10 feet wide.

ditions in San Francisco Bay has been adapted from information in Miller, Ramage, and Lazier (1928).

The progression in range of the highest high tides in the spring of three years may be seen in figure 7. Here also is shown the fact that tides vary in their height one year to the next. With all heights referred to mean lower low water, the general range of the tides at San Pablo marsh is as follows (after U.S.C.G.S., 1949–1954):

Estimated highest tides <sup>1</sup>	7.5-9.0 ft.
Mean higher high water	5.8
Mean sea level	3.2
Mean lower low water	0.0
Lowest expected tide	-2.5

1 Not from U.S.C.G.S. data.

The highest tide data have to be expressed as a range to account for the variation between years and to account for extreme climatic conditions. For example, it occasionally happens that the high tides in December are coupled with heavy rainfall and, infrequently, with winds that push surface water onto the marsh. The height of the tides is accordingly increased, probably from six inches to two feet, and especially so if the rains have been distributed over the entire central California basin, for then the Sacramento-San Joaquin drainage system adds a large amount of water to San Francisco Bay. The highest tide for any year will almost certainly occur in the winter even though June may have as high or higher readings in the tide tables.

The tides may be said to control the distribution of the plant species on the marsh, although other factors also operate. The lower limit to the range of any species seems to be closely related to the amount of submersion it can withstand (see Hinde, 1954), for, when plants are submerged, photosynthesis and gaseous exchange are greatly restricted. The interplay between the physiological characteristics of the plants, the elevation of the soil, and the height of the tides results in the zonation and interdigitation of the two plant associations on the marsh.

Interspecific relationships.—The relationships the Song Sparrow has with other animals and which were investigated in this study may be grouped into three categories: predatory, parasitic, and neutral or undetermined. The first of these is considered later, under "Mortality factors."

The Cowbird (*Molothrus ater*) is the only parasite on the Song Sparrow about which I have information. This parasite is of little consequence in the world of the salt-marsh Song Sparrow. This contrasts markedly with the situation found in Ohio and, presumably, in the eastern United States generally. Likewise it contrasts, but to a lesser degree, with the situation on Wildcat Creek, which flows down from the Berkeley Hills into San Pablo Bay.

On the marsh Cowbirds were seen in 1953, 1954, and 1955. In 1953 and 1955 the incidence was light and the birds seen were mostly single males. Females also occurred on the marsh, but my attention was not drawn to them. The incidence was heavier in 1954, at least one Cowbird being seen on most visits to the marsh from April through June. As many as six were seen one morning in May; this included two females. Notwithstanding this occurrence but two eggs and only one nestling of Cowbirds were seen on the marsh; presumably this means there was little reproduction by Cowbirds in the area.

The reasons for this lack seem obscure, unless they lie in the fact that Song Sparrow nests are difficult to find. Since Cowbirds are probably unfamilier with the vegetation on salt marshes, they may have as much difficulty as do humans in finding nests of Song Sparrows. They can with little difficulty find nests of Song Sparrows along Wildcat Creek; here Cowbirds are in familiar habitat and exist as a true breeding and fairly dense population.

The Red-bellied Harvest Mouse (Reithrodontomys raviventris) has a definite relationship with Song Sparrows. Probably only a part of it has been demonstrated by the present study. It is certain that adult harvest mice use old Song Sparrow nests for shelter and occasionally for their own nesting purposes. For the latter, the mice roof over a Song Sparrow nest and thus construct a fairly typical, spherical mouse nest. Litters of young mice have been found in such nests twice, and a total of five nests has been found in active use by harvest mice. All five sparrow nests used by the mice were of pairs of birds whose nesting attempts had failed early in the cycle, that is, eggs or very young nestlings had been removed by some agency and the nests deserted by the adult birds. The mice avoid nests that are flattened-out or encrusted with feces and excrement or littered with fragmented feather-sheaths.

Twice I have found adult mice using old Song Sparrow nests for shelter in daylight hours. These nests were not modified in any way; the mice were there on a temporary basis. What occurs when a mouse comes upon an actively used but momentarily unoccupied bird nest is not known. Such occurrences must be relatively common and it is probable that the birds drive off the mice. But when the attendant adult Song Sparrow is absent, the mice have a short period of time to themselves. The disappearance of single eggs and nestlings from nests may possibly be laid to the activities of the mice at this time.

The Savannah Sparrow (Passerculus sandwichensis) is an abundant permanent resident of the same marshes in which Song Sparrows live. Because Savannah Sparrows occupy the drier, grassier, upper marsh areas, there is only marginal contact between them and Song Sparrows. On the average about six pairs of Savannah Sparrows have nesting territories on the upper periphery of the area inhabited by Song Sparrows. Additionally, numerous Savannah Sparrows fairly regularly find foraging areas within Song Sparrow territories. But on only one occasion have I seen an act of aggression: a male Song Sparrow flew at a male Savannah Sparrow that was singing in the top of a Grindelia bush in the former's territory. Marshall (1948:204) concluded that, in spite of territorial overlap in edge situations, these two common species are not ecological competitors on salt marshes; my observations have repeatedly supported this.

#### ANNUAL CYCLE

Inception of breeding.—Factors influencing the time of inception of breeding in bird populations are known to be many. Most of them probably will be found to be closely correlated with the biological growing season in temperate regions. It has been demonstrated (Johnston, 1954:272) that there is a close relationship between the inception of the breeding season in several populations of Song Sparrows along the Pacific coast and the march of the biological growing season from south to north (the bioclimatic law of Hopkins). Populations of Song Sparrows are retarded in the inception of breeding by three to four days for each increasing degree of latitude.

Some of the factors that influence the timing of the biological growing season are thought to influence the inception of breeding by direct action on the bird. These are the photoperiod, the temperature of the two months before the breeding season, and probably also that of the preceding winter period (Davis and Davis, 1954:342), and the amount and temporal distribution of rainfall. Probably also very important is the effect of the three factors on the quality of food supporting Song Sparrows.

Other investigators have been able to show a correlation between inception of

breeding and some aspect of the temperature relationships beyond those involved in Hopkins' bioclimatic law. Thus, Nice spoke of a "temperature threshold" which, when reached, was followed by general breeding in the Song Sparrows she studied. Kluijver (1951:54) was able to show that Great Tits (*Parus major*) bred only after a certain amount of heat had been radiated to the surface of the earth; he summed the mean daily temperatures from the first of January to the date of inception of breeding in 16 successive years and found that the minimum "warmth-sum" was around 320°C. His data are very convincing.

I cannot show such correlations between salt-marsh Song Sparrows and their temperature environment. Table 1 shows the progression of temperature sums from Janu-

Table 1

Progressive Summation of Daily Mean Temperature in the Period January 1-March 25
at Richmond, California

		Day degrees	in °Centigrac	le
	1952	1953	1954	1955
Dec. 31	0	0	0	0
Jan. 15	110	185	152	110
Jan. 31	267	373	317	252
Feb. 15	443	559	475	415
Feb. 28	593 <sup>2</sup>	704 <sup>1</sup>	640	551
Mar. 5	646	756	706	604
Mar. 10	696	830	768	6721
Mar. 15	739	883	815	731
Mar. 20	783 <sup>1</sup>	937	863	798
Mar. 25	856	1010	9171	872

 $^1\,\mathrm{Date}$  and temperature at which the earliest clutch was completed.  $^2\,\mathrm{February}$  29 is omitted from the summation; the mean temperature that day was 15.5°C.

ary 1 to March 25 for four years in intervals of 5 to 15 days. The temperature record was not made on San Pablo marsh but in Richmond, about one and one-half miles distant and at a height of 30 feet. All through the four years the summations are very close to one another. The sums have no direct relationship to the start of breeding, but it would appear that a minimum amount of heat necessary to produce conditions favorable to starting breeding is of the order of 650° to 700°C. But I do not want to say that any cause and effect relationship between a threshold or warmth-sum and inception of breeding exists in these birds. Temperature sums for this region for many years would show the same close agreement in summation. This is not a particularly noteworthy fact in itself, for central coastal California has essentially a maritime climate, one characteristic of which is a restricted seasonal and annual variation in temperature.

What importance to initiation of breeding the extremes and sudden shifts in temperature have is yet unexplored.

The influence of amount and distribution of rainfall on breeding is doubtless a complex one in temperate latitudes. It is worth mentioning that total winter-spring rainfall has no apparent relationship to the start of breeding in the present population. It is probable that the distribution of rain through the winter-spring season is as important as the total amount of rain that falls.

All these climatic phenomena influence the amount and nutritional quality of the spring vegetation, the invertebrate fauna of which is most important as food to Song Sparrows in the spring and summer. Factors in addition to the condition of the food

supply that influence the abundance and availability of invertebrates as food include winter temperature, success of the earliest yearly reproductive efforts, amount and distribution of rainfall, and, in the case of insects, the conditions at the time of flight. It is probable that the complex of factors subsumed by the term "food situation" is most important in regulating many aspects of the breeding cycle, including the timing of the start.

It should be emphasized that whatever factors are most instrumental in bringing about the onset of laying in this population they without much doubt act most tellingly on the female birds. As is mentioned later, males are sexually ready for breeding by at least mid-February but the bulk of the females are not ready for mating and laying until about four to six weeks later. Davis and Davis (1954:343) have noted the same thing in the English Sparrow (*Passer domesticus*); it occurs generally in passerine birds at mid-latitudes.

A special set of factors making for early breeding seem to be operative on salt-marsh Song Sparrows. These relate to the tidal fluctuation and are discussed on pp. 33–35.

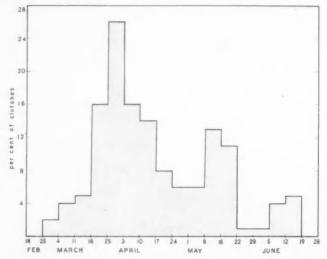


Fig. 5. Frequency distribution of completed clutches of salt-marsh Song Sparrows;  $N=111\ (1952-1954)$ .

Breeding season.—The breeding season in M. m. samuelis is graphically illustrated in figure 5, which shows the span of the season and the frequency of nesting within that span. The birds breed generally from March to June, but they may occasionally go beyond these limits. Figure 5 indicates that there are three populationwide periods of general egg-laying: a main peak early in the season in which most of the birds on the marsh are active (late clutches of this group may actually be renestings), a second peak that involves renesting and second nestings, and a third peak that involves renesting efforts on the part of a relatively small part of the population.

This general picture masks the variation between years. The seasonal incidence of nesting for the same years as shown in figure 5 is graphed in figure 6. There were three nesting peaks in both 1953 and 1954; these followed regularly on one another at four-

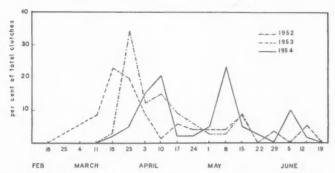


Fig. 6. Frequency distribution of completed clutches of salt-marsh Song Sparrows; 1952, N=31; 1953, N=45; 1954, N=35.

week intervals. Since four weeks is not enough time to rear a brood of young Song Sparrows to independence, it is clear that relatively few successful breeders were involved in the activity represented by the peak following the time of their successful nesting. The four-week interval between successive completions of clutches indicates that these birds wait longer than a day before initiating renesting; Nice found that Ohio Song Sparrows had a new nest with an egg only five days after the destruction of a previous nest, and it takes four days to build a nest.

Table 2
Schedule of Events During the Early Breeding Season in Two Populations of Song Sparrows

	Inception	Inception of breeding		
Population	Earliest date	Mean date	Modal date of first clutches	
San Pablo salt marsh	Feb. 28	Mar. 16	Mar. 28	
North-hay unlands	Mar 25	Apr 1	Apr 15	

Around San Francisco Bay1

It has been noted previously that salt-marsh Song Sparrows breed earlier than upland Song Sparrows at identical latitudes (Johnston, 1954:270); the time involved is of the order of fifteen days (table 2). It seems likely that this early nesting represents an adaptation on the part of the marsh birds to the conditions of tidal flux and wane, since the first and major nesting effort of the population occurs during the time of minimum tidal heights for the whole spring season (fig. 7, data from U.S.C.G.S., 1951–1954). As the graphs of the tidal progression indicate, the maximum heights of the high-high tides in the three years varied strikingly. Nevertheless, the maximum height of the tides bore only a general relation to the mortality caused to young Song Sparrows in any year.

The year 1954 had the highest high tides of the period from 1952 to 1954 and also the highest actual egg-nestling mortality of the three years. But the lower tides of 1952 caused a greater per cent mortality than the higher tides in 1953. The difference is not statistically significant, but it does not invalidate the point that the height of the tide may not stand in direct relationship to the number of young Song Sparrows killed. The

Data from Johnston (1954:272).

most important factor reducing egg and nestling mortality in 1953 seems to be the fact that the population undertook very early general breeding; over 60 per cent of the eggs laid that season had already fledged young before the first serious high tide came over the marsh. The hypothesis is that selection has fitted the Song Sparrows of the marsh to early breeding so that, given a normal set of environmental circumstances, the birds breed before the high run of high tides and thus escape a chief cause of mortality in the young age classes.

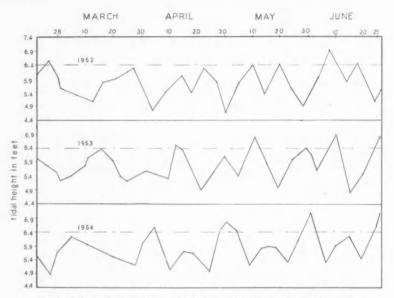


Fig. 7. Variation in the heights of the highest spring tides on San Pablo marsh, 1952-1954.

Most tides that reach 6.4 feet or higher on the marsh are high enough to flood nests of Song Sparrows. Table 3 shows the relationship between tides reaching at least 6.4 feet in three different breeding seasons and the number of deaths caused to Song Sparrows as a direct result of the high tidewater. In the three years the number of days having the high tides varied between 14 and 20 per cent of the total number of days that

Table 3

The Relationship between High Tides and Mortality of Young Song Sparrows on San Pablo Marsh

	Days tide reached 6.4 feet or higher						
Year	Length of season in days	Number	Per cent of season	Number of eggs per season	Youn Number	g killed Per cent	
1952	104	15	14.4	107	8	8.5	
1953	125	24	19.1	140	4	2.8	
1954	99	20	20.2	102	19	18.2	

the population of Song Sparrows was engaged in breeding. At the same time the mortality caused to eggs and nestlings varied from a negligible fraction to almost one-fifth of the total number of eggs laid for the year. There is no correlation between the number of high tides and the amount of mortality to young birds caused by them, according to these data.

With respect to the tides, the pattern of normal nesting activity is as follows: When the tidal cycle is on a downswing, through February, Song Sparrows approach breeding, and males are ready to breed by mid-February; laying usually begins some time in March. The bulk of the population has usually completed clutches by the last week in March and the young of these first nestings leave the nest before the fairly high tides of late April. There follows an upswing of nesting activity in May, the resultant young leaving the nests before the high tides of early June occur. Subsequent to this only sporadic nesting is found in the population and much of this is flooded by the very high tides later in June.

Any low-positioned nest on the marsh stands in danger of being flooded even by such relatively low high tides as those reaching 6.2 feet. Eggs are floated away and nestlings under the age of eight days are drowned; a nestling eight days old is capable of climbing up in the vegetation above the nest and many escape drowning in this manner. Therefore, since June and July have frequent high tides, late nesting probably has no selective advantage in this population, and may actually work to its disadvantage, for nesting activities are physically taxing, and conspicuous, territorial males are more subject to predation. But, early nesting may be considered to be advantageous, for the reasons already outlined.

When the typical early nesting season is delayed, it is abundantly clear that the saltmarsh Song Sparrows suffer drastic consequences. The season of 1954 saw retarded breeding both in salt-marsh and upland Song Sparrows, and by the time nestlings of the marsh birds were in the nest the high tides of late April and early May inundated the marsh; all nestlings under eight days of age were drowned. Of a total of 17 nestlings of all ages under observation at this time, 12 were killed and 5 saved themselves by climbing above the water level. The same thing on a reduced scale occurred in both the second and third nestings and the total seasonal productivity was near the lowest recorded for the population.

The productivity was in fact so low that it did not suffice to maintain the population at the level at which it had been for the two years preceding, and the density in 1955 was 14 per cent below that of 1954. The data on density and productivity will be presented later.

Nests are placed off the ground in all cases, most commonly in Salicornia, Grindelia, Distichlis, and Spartina. Since the average height of this vegetation is less than two feet, nowhere can the birds nest in high places. Yet nests placed lower than five inches above the ground surface are flooded. It is not by chance then that nests average about nine and one-half inches high over the whole marsh and about twelve inches on the lower marsh. Nests are most frequently placed as high in a particular site as they can be and still be afforded the vegetational cover that is apparently necessary for the nest contents and the adult occupant. However, the birds do not often choose for the nestsite the tallest vegetation available to them in a given territory; predators, mostly mammalian, probably also exert a selective pressure to the end that Song Sparrows use those sites suited to meeting the whole environment. Nests are never used twice and the several nests of any one season are placed in different parts of the territories.

Generally, with the increase in the height of the vegetation as the breeding season progresses, it is possible for the birds to nest at successively higher levels. This parallels also the increase in tidal heights through the season. Data are sparse on this point, but in June no nest lower than ten inches off the ground has been found.

It is difficult to estimate accurately the number of times a pair of salt-marsh Song Sparrows nests in one breeding season. It is more difficult to find every nest of ten or twenty breeding pairs in one season and thus speak of averages. I know with certainty that practically every pair will nest twice in any season. The data of Nice (1937:134) show that for the year 1930 twelve of the pairs she watched in Ohio nested three times in the season and four pairs nested four times. The average number of nestings per pair was 3.25 per season.

I include these figures to indicate the general expectancy of number of nestings per season. Since nests of salt-marsh Song Sparrows are difficult to find and since observations indicate many nestings for which I have no record, I have assumed that each pair of birds had one more nest that I was unable to detect. Moreover, if a pair was observed to have two nests before half the breeding season was over, I have credited them with an additional nesting effort. Averages calculated on these bases are 2.5 nestings per pair in 1952, 1954, and 1955 and 3.0 nestings in 1953. These guesses do not seem high if it is considered that all nesting attempts are included, not just the successful ones.

Clutch-size.—Clutch-size is another characteristic that has been found to vary between populations of Song Sparrows. The birds of San Pablo marsh have a lower clutch-size than that found in any other population of Song Sparrows at comparable latitudes across the United States. The only population that resembles samuelis is that found on the lower reaches of San Francisco Bay, namely pusillula (Johnston, 1954:272); since this group too lives in a salt-marsh environment, it appears that the factors operating to control the size of clutches are the same in the two marsh areas. Further, the physiologic response on the part of the two races of birds must also be similar.

Lack (1946, 1947a, 1947b) has already given an indication of the variation in clutch-size to be found inter-seasonally and intra-seasonally, between birds-of-the-year and adults, and geographically for many species of birds, and Kluijver has catalogued similar variations for local populations of the Great Tit.

Table 4

Variation in Clutch-size in Song Sparrows on San Pablo Marsh

				Time of y	rear			
	Feb. 28-	Apr. 5	Apr. 6-1	May 25	May 26	July 1		
Breeding season	Number of nests	Mean clutch	Number of nests	Mean clutch	Number of nests	Mean clutch	Seasonal mean $\pm \theta$	S. D.
1950-51	9	3.22	6	3.66	1	3	$3.37 \pm 0.12$	0.48
1952	14	3.35	16	3.56	1	3	3.42 ±0.10	0.57
1953	27	2.92	14	3.29	4	3.25	$3.04 \pm 0.09$	0.61
1954	6	2.83	24	3.00	5	2.60	$2.91 \pm 0.09$	0.56
1955	9	3.11	17	3.23	4	3.50	3.23±0.09	0.50
1950-55	65	3.08	77	3.23	15	3.07	3.20±0.05	0.60

It is apparent from the data in table 4 that average clutch-size is occasionally an oversimplification, for it masks important seasonal and yearly shifts in clutch-size. There is first the typical seasonal progression in clutch-size from a low value early in the season to a high in mid-season, dropping again lower at the end of the season; this pattern has been noted in a variety of passerine birds and is linked presumably to the food situation (Lack, 1947a). Secondly, there is evident a yearly shift in the size of clutches.

Annual variation such as this has many controls; known and hypothetical controls for salt-marsh Song Sparrows are diagrammed in figure 8.

I believe Lack is right in postulating that the size of the clutch with regard to yearly variation is a reflection of the number of young that the adults can successfully rear at one time; certainly the data on brood size and nestling survival in the Common Swift (Apus apus) strongly support the thesis (Lack and Lack, 1951:517). The proximate factor controlling clutch-size can now only be guessed at, in the absence of critical physiological data, but the major environmental variant that impinges on a pair of birds in nesting and rearing a brood of young is the availability and quality of food.

Even though this may almost be taken as a truism, little direct evidence can be found to support it. Lehmann (1953:225) has shown the seasonal decrease in clutch-size in the Bobwhite (Colinus virginianus) is paralleled by the amount of decrease of stored vitamin A in the liver. This is all the more suggestive when it is considered that he also found that a reduction in the amount of vitamin A in the diet of the Bobwhite retards the inception of breeding and may even prevent some individuals in a population from breeding at all in a given year. This happens in years that have low spring rainfall with a subsequent stunting of green vegetation, which is the birds' main source of vitamin A prior to breeding.

These correlations merit serious consideration in any theory on the control of annual variation in clutch-size, although more evidence obviously is needed for any one species; certainly other aspects of the qualitative nature of food may be also operative.

The low clutch-size (table 4) recorded for Song Sparrows in mid-season of 1953 should be mentioned here. At the time that the birds were initiating these clutches, for second and re-nestings, there was already a major increase in population number due to the production of young from the earlier and numerous first nestings. Possibly this increase in the number of Song Sparrows on the marsh left the increased food supply expected at that time again in relatively short supply. It is perhaps in this way that population density influences clutch-size: there is an interplay between a fluctuating food supply and a fluctuating abundance of birds, in which the absolute number of items in either category is less important than the balance obtaining between them.

Figure 8 diagrams the possible relationships between the several factors that may influence annual and seasonal variation in clutch-size in salt-marsh Song Sparrows. The relationships, although possibly obvious, are also sufficiently complex as to deny simple analyses. As a general rule in nature, a reduced mortality rate does not in itself mean a species or population will have a higher density of population. Yet in salt-marsh Song Sparrows, one year's density depends largely on the preceding year's production of fledglings; this in turn is largely influenced by mortality of young in the nests. Evidence for this will be presented in Part II.

A high population density seems certain to work to reduce the relative amount of food available to any given female bird, probably through constriction of the size of the territory; in these birds the size of the territory varies with density. Variations in density may also make themselves felt in other, as yet unknown, ways; I have grouped these hypothetical effects in the box labeled "psychological state."

The physiological effects, along with the psychological effects, are catch-all categories, reflecting ignorance concerning proximate determinants of clutch-size. So, to a lesser degree, is the term "individual genetic limits" a reflection of our ignorance. But it may be assumed that such things as the average annual mortality rate, the general food situation with respect to the number of young that may be fed, and the number of eggs that can be covered by the sitting bird have a causal relationship in the determination of genetic limits of clutch-size for a species.

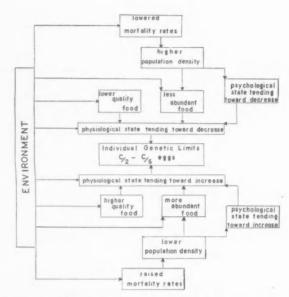


Fig. 8. Factors influencing annual and seasonal variation in clutch-size of salt-marsh Song Sparrows.

Territory and movement of adults.—Territorial relationships of Song Sparrows on San Pablo marsh are typical of those of the species elsewhere. There is only a slightly earlier inception of most features of the annual cycle. In late winter and spring there is evident a rise in the incidence of songs of males and of other aggressive habit patterns, such as pursuits. By late February and early March territories are set out by almost all males on the marsh. There are usually a few trios yet to be found in areas that normally would comprise a territory at this time, but these situations are resolved at the latest by the first of April.

Singing decreases during the latter half of March and in April. Territorial strife as manifested by chases and periodic singing is to be noted during the whole of the breeding season, but these occurrences are momentary and are not a large part of Song Sparrow activity at this time. Following breeding and beginning with the inception of molt in early July there is an almost complete cessation of territorial activity. It is during this period of territorial inactivity and that time immediately preceding it that juvenal Song Sparrows disperse through the population; it should be noted that juvenal birds are tolerated in breeding territories in April and May; aggression is restricted to adult birds.

In late August and into September, when molt is almost completed, there is a noticeable rise in territorial activity. Both birds-of-the-year and adults become more aggressive. One result of this, apparently, is to bring to a halt further dispersal of young birds. But, true territories are not staked out, for in some cases three to six birds are found in an area normally comprising one breeding territory. These groups possibly are comparable to the groups Nice (1937:63) recorded in winter; it is certain that they are not

family groups. However, in the majority of cases two birds, a pair, will be found in each such area.

By the time of breeding in the following year, occupants of territories are reduced to a complement of two, or, rarely, three birds. The extra birds are, without much question, young-of-the-year; probably also they are males. In all instances two of the three birds contended for territorial possession and the third individual qualified merely as an interested onlooker. The latest date on which any trios have been seen has been during the first week of concerted breeding activity in any year; a specific date is March 26, 1954. I do not know what happens to the extra birds except that eventually they disappear from the territories. It seems likely that some fall to predators or move only slightly to a neighboring area if the opportunity presents itself. It is certain that the birds do not move far if only one banded bird has been found to move under such circumstances.

Indications from previous studies are that Song Sparrows are highly sedentary with respect to the breeding territory (Nice, 1937; Miller, 1947). Salt-marsh Song Sparrows have an extremely strong attachment to the breeding territory; this is evident throughout the year. The birds are found in the area of the breeding territory (the "domicile" of Kluijver, 1951:22) even when territory is not actively being defended. Doubtless this high degree of "ortstreue" is related in some way to the essentially non-migratory habit of these birds. It would appear to be easier for a bird to remain in its territory of the previous year if it ventured away no more than 100 or 200 yards, than if it undertook migration.

The closest approximation to migratory movements shown by Song Sparrows of San Pablo marsh occurred in a small area of tall *Salicornia* on the high marsh, where, in 1952 and 1953, the birds bred. In the summer of those years the birds moved out and returned only in winter when the area became moist enough due to the winter rains. In the dry years of 1954 and 1955 there was no occupation of or breeding in this area. I consider this to be an irregular occupation of a marginal habitat rather than true migration. I have included none of the individual birds that moved this way in the data in table 5 on movement of adults, for movement on the lower marsh, where habitat changes are minor through the year, if of a different nature.

Table 5

Changes in Position of Territory of Adult Salt Marsh Song Sparrows from One Breeding Season to the Next

Distance moved 1	Males	Females	Total:
0-15	27	16	43
16-25	1	2	3
26-35	1	1	2

<sup>1</sup>Center to center of territory. <sup>2</sup>Forty-eight cases but 24 birds; see text.

Table 5 shows the distance between centers of breeding territories in successive years for 24 Song Sparrows. Individual birds appear in the table one or more times, depending on the number of years they held territory according to my records. The 24 individuals furnish 48 records of possible movement from one year's territory to the next. Roughly one-ninth of the sample is seen to have undertaken movement of a relatively short distance. This is a significant part of the whole, but the importance of this to the structure of the population is reduced by the fact that the movement is on such a minor scale. von Haartman (1949:62) used 0.10 kilometer as his smallest unit in dis-

cussing movement of adult birds of several species; this unit is too large for analysis of the present data. Basically the important fact obtained from the data is that the movement is almost wholly of a scale less than the dimensions of a territory; eight birds that moved averaged 16 meters each.

Dispersal of juveniles.—The major means by which transfers of individuals occurs between populations of non-migratory Song Sparrows is dispersal of young birds. This probably also is true for most species of non-migratory birds, for young birds are not attached to their places of origin as are adults to their breeding territories. Dispersal, or movement by young from their places of birth to their places of eventual breeding, is an important adaptation for all sedentary species of animals, if not for more mobile ones, for its existence ensures a tendency in time toward a greater degree of panmixia than otherwise would be possible; there is, in Miller's (1947) expression, a graded panmixia in space and time.

This means that a large population consists of relatively small completely interbreeding subunits in any given breeding season. According to present theory (Wright, 1932:361; 1950:247) this is a favorable situation for maintaining a genetically healthy population, since none of the subunits exists genetically isolated in time long enough to allow fixation by chance of deleterious alleles, yet varieties of genetic combinations

are given opportunity, so to speak, to demonstrate survival value.

In salt-marsh Song Sparrows dispersal by the young takes place in the summer of the year, or when the birds are at least one month old but probably before they are two months old. Individuals disperse independently of one another; Goodbody (1952;285) and Gibb (1954:44) noted an "explosive" or sudden dispersal in banded titmice (Parus) when they reached three or four weeks in age. After August and September no additional effective movement occurs among Song Sparrows. That this apparent attachment to what amounts to the future breeding territory takes place in a bird's third or fourth month of life is not surprising, for in August each year there is a marked upswing in territoriality; this would tend to inhibit further, indiscriminate wandering through the marsh. In titmice neither Goodbody (loc. cit.) or Kluijver (1951:30) noted such a cessation of movement; dispersal with these species continued to February or March.

In graphing the records of dispersal (fig. 9) I have included data obtained from individual banded Song Sparrows observed from August through to the following breeding season, regardless of the fact that some of the individuals seen before the time of initiation of strict territoriality in the spring did not live to breed. Nineteen of the 34 records are for such birds. A comparison of the territorial and non-territorial groups shows that there is no difference between them in the median distance of dispersal, but a slight although statistically insignificant difference in the less meaningful average distance of dispersal. One bird did move from the area it had ostensibly dispersed to in September; in the following March the bird was found 150 meters distant. The "original" distance of dispersal was 185 meters, the final 300 meters.

In converting the field observations to quantitative data I measured with finepointed dividers the shortest straight-line distance between the two areas involved in dispersal for any one individual on the United States Production and Marketing Administration aerial photograph number BUU-9G-57, which covers San Pablo marsh.

This measure was converted to linear distance.

The absence in this sample of juvenal birds moving 500 to 600 meters deserves special comment. In the first instance, there are proportionally fewer spots on the marsh 500 to 600 meters from nestsites, which also are habitable by Song Sparrows, than there are those that occur less than 500 and more than 600 meters. This is due to the vast expanses of low Salicornia on the upper marsh. Secondly, there is apparently a tendency for the birds to follow the courses of the tidal sloughs, along which their preferred cover grows; there is less of a tendency for the birds to leave the sloughs and cross open ground, but this occasionally they do. Another possible reason for this gap in the records of dispersal is that juvenal birds may be differentially endowed with an instinct to disperse. This suggestive line is pursued beyond.

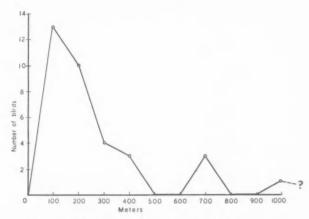


Fig. 9. Distance of dispersal of juvenal salt-marsh Song Sparrows, hatching site to breeding site.

The data shown in figure 9 represent dispersal of the most limited degree yet found in any bird population. The median distance of dispersal is 185 meters, about 100 meters less than that found for Ohio Song Sparrows (Miller, 1947:188). The extreme distances recorded for the salt-marsh birds are 30 and 960 meters. Forty-two per cent of the juveniles settled within 150 meters of their point of origin, 66 per cent within 250 meters, and 81 per cent within 360 meters.

One other example that approaches this pattern of dispersal is that found in European populations of the Starling (*Sturnus vulgaris*) as detailed by Kluijver (1935), but the median distance of dispersal for this population was close to 400 meters, and the mean over 500 meters. Farner (1945:91), von Haartman (1949:63), Kluijver (1951: 14), Kendeigh (1941:18), Lack (1953:116), and Ruiter (1941) all dealt with species that showed dispersal to great distances.

It remains yet to examine the dispersal to see whether these results are a function of directed movement or if they may have occurred at random. The random occurrence of isolated events in a continuum is effectively described mathematically by the Poisson distribution; if the distribution of these salt-marsh Song Sparrows parallels that calculated by the Poisson distribution, then it may be assumed that this dispersal is random and undirected.

I have calculated Poisson distributions using the present data and Mrs. Nice's data for the Ohio Song Sparrows and have compared them with the observed cases of dispersal in both populations (table 6). The Ohio population has been included here for comparison with the salt-marsh population, for the similarities are striking and suggestive of a common pattern. Both groups of Song Sparrows are found to have curves describing their dispersal that differ from expectation significantly at the one per cent

Table 6
Observed and Computed Distribution of Dispersal in Two Populations of Song Sparrows

	Distance of dispersal in meters								
	100	200	300	400	500	600	700	800-	
California									
Per cent expected	30.6	25.6	20.7	12.4	5.9	2.3	0.7	1.8	
Per cent observed	39	30	12	8	0	0	8	3+	
Ohio									
Per cent expected	22.8	23.5	22.8	15.5	8.6	3.3	1.0	2.5	
Per cent observed	12	27	30	8	6	8	3	6	

level. For the California sample, the main characteristics of the observed curve of dispersal that deny a random nature are that fewer birds move to intermediate distances (350 to 650 meters) and more birds move to distances beyond 650 meters than the Poisson distribution requires. There is also a tendency for the birds to aggregate more than expected at the lower end of the curve, but it is possible that the results listed here could have occurred by chance, as chi-square gives significance only at the ten per cent level.

It is to be noted that about ten per cent of the Song Sparrows in both the California and Ohio samples moved to the greater distances; possibly this mirrors a definite drive in this small part of the whole to move great distances. On this basis it would have to be assumed that the bulk of the dispersing juveniles have no strong drive to move anywhere. This is not inconsistent with the fact that no other bird species has so restricted a dispersal; the young of such species as Troglodytes aëdon (Kendeigh, op. cit.), Phoenicurus phoenicurus (Ruiter, op. cit.), Muscicapa hypoleuca (von Haartman, 1949:60), and probably also Saxicola rubetra (Schmidt and Hantge, 1954) have very little tendency to aggregate, dispersing uniformly to great distances through suitable habitat. The proposed existence of a small fraction of the juveniles that are hereditarily endowed with a tendency to disperse to great distances merits comment. The fact that both the salt-marsh and Ohio Song Sparrows show a group of juveniles that move great distances suggests that this is a real phenomenon. Reasons for this peculiarly endowed fraction of the population may be found in the selective advantages of gene interchange between semi-isolated populations, as expanded by Wright. Noteworthy also is the hypothesis of a similar basis for long-distance dispersal in Peromyscus by Dice and Howard (1951).

# SUMMARY

A population study of Song Sparrows of the race *Melospiza melodia samuelis* was carried out in the years 1950–1955 on San Pablo salt marsh, Contra Costa County, California, by means of color-banding; 287 individuals were banded.

San Pablo marsh is a typical San Francisco Bay salt marsh, grown to a *Spartina* association on lower levels and a *Salicornia* association on higher ground. The tidal range is -2.5 to 9.0 feet; mean higher high water is 5.8 feet.

Factors influencing the initiation of breeding in the Song Sparrow are closely associated with the biological growing season and include the photoperiod, temperature of the preceding three months, and the amount and distribution of the winter rainfall; these influence also the amount and quality of the Song Sparrow's food, which may well be the most proximate factor. The inception of breeding seems not to be closely related to any "temperature threshold" or "warmth-sum."

Breeding spans the period from March to June; the peak of first nestings is March 28. This is more than two weeks earlier than in upland Song Sparrows at the same latitude; this seems to represent an adaptation to marsh life, for the birds thus nest mainly

during lower tidal conditions. It is shown that it is not the absolute height of the tides that governs egg and nestling mortality, but whether or not the birds can nest early enough to escape the high run of tides in April to June; when they breed late, there is high mortality caused by the high tides.

Clutch-size in this population averages 3.20 eggs, but may be as low as 2.91 (1954) or as high as 3.42 (1952). Environmental variations that induce variation within the genetically determined limits of clutch-size are thought to include quality and quantity of food, population density, and mortality rates.

Male Song Sparrows set up territory through the late fall and winter and are completely territorial by late February. Territorial defense is lacking from July to September when the adults molt; autumnal territoriality is seen in mid-September. Adult birds rarely shift territory from one breeding season to the next, and of eight that did the average distance, center to center of territory, was 16 meters. Dispersal of juveniles occurs in the late spring and summer and halts in late August and September when territorial activity rises. The median distance of dispersal, hatch-site to breeding-site, for 34 Song Sparrows was 185 meters. The limited adult movement and restricted distance of dispersal of these Song Sparrows mark them as the most sedentary population of birds yet investigated. Nearly 10 per cent of the juveniles seem to have a tendency toward dispersal to relatively great distance.

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# LIVER AND SPLEEN WEIGHT CYCLES IN NON-MIGRATORY WHITE-CROWNED SPARROWS

## By BARBARA BLANCHARD OAKESON

Modern field studies on nutritional states of migrating birds, such as those of Irving and Paneak (1952), have cast doubt on the idea that migration is a period of stress. The facts in this paper bear indirectly on this question and support the suggestion (Oakeson, 1954) that it is not stress involved in the long flight north, but, rather, inherent endocrine changes that are responsible for the low body, liver and spleen weights of male White-crowned Sparrows (Zonotrichia leucophrys gambelii) arriving in May at Mountain Village, Alaska. The sharp decline in organ weights between April and May in Z. l. gambelii coincides not only with migration but with the period of most rapid testis development (Oakeson, 1953). To find out whether this decline is a concomitant of gonad recrudescence per se, I analyzed liver and spleen weights in the permanently resident form, Z. l. nuttalli, for the corresponding period. This race is ideal for such comparisons, since its gonad cycle is, except for timing, identical with that of gambelii.

#### ACKNOWLDGEMENTS

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#### MATERIAL AND METHODS

I was fortunate in finding at Guadalupe, Santa Barbara County, California, areas where White-crowned Sparrows of the race nuttalli were abundant and could be banded in early fall. Identification of this race in winter is complicated by the presence of the morphologically similar migratory race, Z. l. pugetensis. One hundred and forty-seven nuttalli were banded, before any pugetensis arrived, in the fall of two successive years. When the latter did come, they kept close to cultivated fields and shunned the more nearly natural vegetation of the trap-sites, where nuttalli abounded.

Between November and March of three seasons, eighty-seven specimens were collected. For the gonad cycle, this period corresponds in *nuttalli* to that between January and May in *gambelii*. These specimens comprised three groups of birds which could be assigned with certainty to the race *nuttalli*: birds banded in early fall (31 specimens); birds taken in January or later with gonads larger than those of any *pugetensis* taken in the month in question (46 specimens); and birds taken on ground where only individuals singing the local *nuttalli* song-pattern occurred (10 specimens). Trapping methods and analyses have been previously described (Oakeson, 1953). The birds taken in mid-March had to be shot, since they do not trap readily at this stage. The comparative figures given in this paper for *gambelii* are based on 200 specimens, collected at Santa Barbara, California, and Mountain Village, Alaska.

All calculations include adults and birds of the year. In neither race is there any significant difference between the two groups as to body dimensions, and in the large number of *gambelii* previously analyzed, no consistent difference between age groups as to liver and spleen weights was found.

In tables 1 and 2 and figure 1, the data are grouped by months. Then, to check whether a direct relation exists between testis volume and ratio of liver to body weight regardless of collection date, I grouped the males of each race in seven arbitrarily de-

Table 1 Monthly Means of Body, Liver and Spleen Weights in  $Z.\ l.\ nuttalli$ 

			Males		
Month	Number	Body weigh Extremes	t (gm.) Mean	Liver Extremes	weight (mgm.) Mean
Nov.	14	25.1-30.6	27.59±0.37	739-1136	919,2±31.6
Dec.	11	26.8-29.5	28.35±0.90	918-1099	987.5±15.7
Jan.	8	27.0-31.6	28.94±0.43	928-1159	1047.9±24.3
Feb.	10	27.3-30.4	28.95±0.29	950-1330	1087.0±35.2
Mar.	12	25.4-31.0	28.30±0.48	772-1107	932.9±37.9
Month	Number	Ratio, liver to body weight (per cent	) Extremes	ght (mgm.) Mean	Ratio, spleen to body weight (per cent)
Nov.	14	3.33	25-65	36.2±3.1	0.13
Dec.	11	3.48	21–56	36.5±3.4	0.13
Jan.	8	3.62	36–89	52.4±5.6	0.18
Feb.	10	3.75	14-45	$30.1 \pm 2.7$	0.10
Mar.	12	3.30	17-51	$27.5 \pm 2.7$	0.10
			Females		
Month	Number	Body weig Extremes	ht (gm.) Mean	Liver Extremes	weight (mgm.) Mean
Nov.	6	24.4-25.3	24.97±0.25	739- 954	836.3±25.6
Dec.	2	25.9-26.9	26.40±0.35	880- 921	$900.5 \pm 14.5$
Jan.	5	25.2-27.1	26.10±0.33	848-1058	954.8±37.5
Feb.	5	24.2-28.8	26.54±0.67	913-1085	996.6±33.3
Mar.	7	24.5-26.7	25.71±0.29	849-1198	950.4±32.4
Month Nov.	Number 6	Ratio, liver to body weight (per cent) 3.35	Spleen weig Extremes 23-48	ht (mgm.) Mean 31.7±3.2	Ratio, spleen to body weight (per cent) 0.13
Dec.	2	3.41	37-49	43.0±4.3	0.16
Jan.	5	3.67	26-79	50.0±7.6	0.19
Feb.	5	3.76	13-75	41.8±9.5	0.16
Mar.	7	3.70	22-37	28.7±2.5	0.11

limited categories of testis volume and calculated the means of testis volume and ratio of liver to body weight (table 3). Since for testes below 3.00 mm.³, size is not a reliable criterion of histologic stage, not all specimens in the second category are necessarily further advanced histologically than those in the first. From category III on, however, the higher the category, the more advanced the histologic stage. This method is especially valuable for *nuttalli*, which shows high individual variability. For example, testis volumes of six adult *nuttalli* collected at Guadalupe on the same day in February, 1953, ranged from 4.41 mm.³ to 75.94 mm.³. Those of three birds of the year collected on March 14, 1953, ranged from 8.62 mm.³ to 130.97 mm.³

#### RESULTS

The outstanding fact revealed in table 1 is that both sexes of *nuttalli* show cyclic changes in monthly means of liver and spleen weights comparable to those in *gambelii* as to direction, magnitude, and timing with respect to the gonad cycle. In males (table 2 and figure 1), the similarity extends to the detail that in spring the highest value for mean spleen weight is reached a month ahead of that for mean liver weight. The curves

for monthly means of body weight are also comparable as to direction and timing but not as to magnitude, since *nuttalli* does not show the cycle of fat accumulation that migratory White-crowned Sparrows do. For the males of *nuttalli*, the standard errors indicate the chances to be about 95 to 5 that the increases in body weight and in liver weight between November and February are statistically significant. The decrease in liver weight between February and March, and in spleen weight between January and February have the same high probability of significance, and the increase in spleen weights between December and January falls only slightly short of this. The smaller numbers of females collected do not warrant comparable statistical analyses.

Table 2

Monthly Means of Body, Liver and Spleen Weights in Males of gambelii and nuttalli for Comparable Segments of the Gonad Cycle

Race	Month	Number	Total body wt. (gm.)	Liver weight (mgm.)	Ratio, liver to body wt. (per cent)	Spleen weight (mgm.)	Ratio, spleen to body wt. (per cent)	Testîs volume (mm.3)
gambelii	Jan.	29	26.67	990.0	3.71	46.3	0.17	0.49
nuttalli	Nov.	14	27.59	919.2	3.33	36.2	0.13	0.59
gambelii	Feb.	17	26.40	949.9	3.60	42.5	0.16	0.50
nuttalli	Dec.	11	28.35	987.5	3.48	36.5	0.13	0.42
gambelii	Mar.	33	27.29	1025.5	3.76	46.8	0.17	1.01
nuttalli	Jan.	8	28.94	1047.9	3.62	52.4	0.18	3.85
gambelii	Apr.	35	28.31	1084.3	3.83	40.1	0.14	1.48
nuttalli	Feb.	10	28.95	1087.0	3.75	30.1	0.10	15.00
gambelii	May	8	25.94	775.4	2.99	19.6	0.08	148.99
nuttalli	Mar.	7*	28.59	873.7	3.06	26.4	0.09	155.45

= maximum

=== = minimum.

\* Only those specimens comparable in mean testis volume with gambelii of Mountain Village are included in the March averages.

Table 3 shows the same tendency in both races for a rise in ratio of liver to body weight through the first three or four categories of testis volume followed by a decline. In both races, the lowest mean value for ratio of liver to body weight falls in category VII. The highest mean values coincide almost as closely: in *nuttalli* the high point falls in category IV. In *gambelii*, where no material for category IV is available, it falls in category III.

One other variable not directly connected with testis volume changes must be considered. The birds of both races in category VII and the <code>gambelii</code> in category VI were shot, whereas almost all those in other categories were trapped. To assess the effect, if any, of differences in methods of collection would necessitate trapping large numbers of birds in category VII. This is not feasible. The available evidence does not suggest, however, that differences in collection methods affect the liver weights to any appreciable degree. First, since all <code>gambelii</code> included in the averages for categories I through III were trapped, the rise in mean liver weights cannot be due to differences in collection.

Table 3

Mean Liver Weight in Relation to Testis Volume in gambelii and nuttalli

Category of testis	Volume range	Nun	nber	Mean vol. (	testis mm. <sup>3</sup> )	Mean wt. (r	liver ngm.)	Ratio, to bod		Histologic stages
volume	(mm.3)	gamb.	nutt.	gamb.	nutt.	gamb.	nutt.	gamb.	nutt.	included
I	0.90- 0.50	56	12	0.34	0.36	922.7	969.8	3.65	3.48	1, 2,
II	0.51- 1.83	74	15	1.00	0.79	1028.1	941.1	3.73	3.35	and 3
III	1.84- 5.00	11	6	2.31	3.56	1091.1	1052.5	3.79	3.70	4
IV	5.01- 20.00	****	12		7.26		1083.5		3.74	5
V	21.00- 56.00	(1)	3	(55.8)	41.59	(752)	1065.7	(2.91)	3.68	6
VI	75.00-131.00	3	2	120.25	103.46	846.3	995.5	3.26	3.51	7
VII	132.00-251.00	4	5	194.10	180.79	728.0	801.4	2.79	2.76	7
	= maximum.									

Second, the mean ratio of liver to body weight for four gambelii shot between April 3 and April 10, 1954 (3.24), is too close to that for nine gambelii trapped during the same period (3.30) to suggest any wide discrepancy attributable to collection methods. Furthermore, no consistent difference in ratio of liver to body weight was found between shot birds and trapped birds with closely similar testis volumes.

To summarize, the results reveal a cycle of liver and spleen weights in *nuttalli* closely similar to that for the corresponding period of gonad development in *gambelii*. This casts further doubt on the concept of migration as a strenuous journey taxing the energy reserves of the bird. On the basis of the admittedly incomplete picture which weights alone reveal, we can say that if the energy reserves of *gambelii* are taxed by flying to Alaska, those of *nuttalli* appear to be taxed about as much by staying home. Actually, the seasonal changes in means of organ weights shown here probably do not reflect stress but rather an endocrine rhythm common to migrants and permanent residents alike.

#### DISCUSSION

With what events in the annual cycle of nuttalli do the declines in spleen weight and in body and liver weights coincide? Assuming that stages of behavior at Guadalupe are identical with those of the same race at Berkeley, California (Blanchard, 1941) and that timing in years of average weather conditions is about the same, then the decline in spleen weights between mid-January and mid-February would coincide with a time of intense competition. Young males would be establishing territories and seeking mates; adults would be defending territories and mates acquired in previous years. Such observations of behavior as I made at Guadalupe in January and February confirms these suppositions. The decline in body and liver weights between mid-February and mid-March should, in contrast, coincide with a period of orderliness and relative calm. Most birds should be mated, the patrol of boundaries should be temporarily in abeyance, the females should be building nests, and there would of course be no young. That the pairs at Guadalupe collected in mid-March had achieved this stage was shown by the lack of loud singing, the absence of disputes, and the frequent utterance of the "seep" call note. This is given by males whose mates are engaged in nest building. It is probable that copulation was also taking place.

The low point in body and liver weights falls, therefore, within a period of reduced activity, when the energy demands imposed by membership in the average sparrow community should be less than they had been a month before and less than they were to be a month later, when there would be young to feed. Studies such as Pearson (1954)

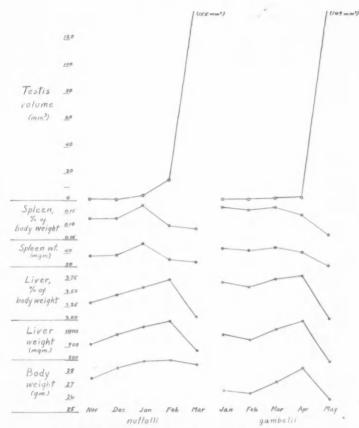


Fig. 1. Cyclic changes in organ weights of resident and migratory White-crowned Sparrows.

is conducting on the metabolism of native species should ultimately permit more accurate assessment of the energy requirements for specific phases of the breeding cycle.

Knowledge of the chemical basis for the liver weight changes is also needed. Odum and Perkinson (1951) analyzed the total body lipids of White-throated Sparrows (Zonotrichia albicollis) and the lipid content of eight body parts, including the liver. They found that subcutaneous lipids are an accurate index to total lipids, and that, except for the heart, all body parts varied seasonally in the same manner, but not necessarily in the same proportion, as did the total body lipids. Values for total lipids in livers of White-throated Sparrows for the four seasons, expressed as percentage of fresh weight of the organ, were as follows: postmigration, 6.4 per cent; midwinter, 10.4 per cent; molting period, 7.9 per cent; and premigration period, 10.6 per cent. Indirect measurements indicate that the water content of the fatty tissues was greater in spring than in winter. Thus weight changes do not completely reflect lipid changes.

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If weights of subcutaneous fat and of total fat show a straight-line relationship in *Zonotrichia leucophrys* as they do in *Zonotrichia albicollis*, then we have one hint of the chemical basis for the increase in liver weights in *gambelii* during the premigration period. Another indirect indication is provided by Musacchia (1953), who found that in the premigration period of late summer there was a high level of fat turnover in four species of arctic migrants. Similar analyses of tissue lipids should be made for permanently resident forms. Since the rise in liver weight in *nuttalli* is not accompanied by increase in subcutaneous fat, substances other than lipids may be involved. It would be highly desirable to analyze the liver for total nitrogen and for glycogen.

For the present, in so far as White-crowned Sparrows are concerned, we can say that, whatever may be the energy demands on the organism during the period of most rapid gonad development, the pattern of liver and spleen weight changes is basically the same, whether the bird flies three thousand miles north or stays on the same spot. The low values for body weight and liver and spleen weights in Zonotrichia leucophrys gambelii newly-arrived at Mountain Village, Alaska, were therefore not necessarily signs of stress imposed by the flight north. From the indirect evidence presented here, migration appears to play a relatively minor part in determining the nutritional state of gambelii as it arrives on its breeding grounds.

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# A SYSTEMATIC REVIEW OF THE MOUNTAIN CHICKADEE

#### By WILLIAM H. BEHLE

Chickadees of the species *Parus gambeli* have a range restricted to western North America where they occupy mountainous country from the Rocky Mountains west to the Cascade-Sierra Nevada cordillera and the interior coast ranges of California and south through the mountains of southern California to the Sierra San Pedro Mártir and Sierra Juárez of northern Lower California. Mountain Chickadees are essentially resident birds showing no pronounced migratory movements although some individuals move to lower elevations in fall and winter, and occasionally vagrants wander out of their breeding range. The habitat of the species is in general coniferous forest, where it breeds from the lowest altitudinal levels of this ecologic type up to timber line.

Being widely distributed over a diversified geographic area and thus being subject to varying environmental influences, the species is composed of several populations of subspecific rank. However, the distinctness and geographic limits of some of these races have been in doubt. It has been the purpose of this study to analyze variation in the principal external characters of the species, determine more precisely the ranges of the races, inquire as to the degree of differentiation and the relationships of the subspecies, and thus to extend our knowledge of the evolution of the species.

For the loan of comparative material which has made this study possible I am indebted to A. M. Bailey, Denver Museum of Natural History; the late A. J. van Rossem, and Thomas R. Howell, Donald R. Dickey Collection, University of California at Los Angeles; Robert T. Orr, California Academy of Sciences; Alden H. Miller, Museum of Vertebrate Zoology; and John W. Aldrich and Herbert Friedmann, United States National Museum. The figures were prepared for publication by my colleague, W. W. Newby, to whom I express my appreciation. Acknowledgement also is made of aid in revision of manuscript and statistics by Robert K. Selander.

## METHODS

Linear measurements were taken in millimeters as follows: chord of the wing; tail from point of insertion between the middle rectrices to the tip of the longest rectrix; length of bill from anterior edge of nostril to tip of the maxilla; depth of bill from anterior edge of nostril to lower edge of mandible in same transverse plane; and width of bill at base. In the course of the study the measuring of tarsal length and length of middle toe was discontinued because of generally unsatisfactory and insignificant results.

Statistical analyses of the measurable characters are presented for each race in tabular form and comparisons are made graphically between the several races following the method described by Dice and Leraas (1936) as modified by Pitelka (1951) and Davis (1951). The samples for each race do not include intergrades but do include both breeding and winter birds taken within the range of the subspecies, since they are resident. Only the measurements of postjuvenal specimens were used. Where the wing and tail feathers were badly worn they were not measured. Juveniles can be distinguished by their loose, fluffy feathers and abbreviated bills. In those few instances where immature birds (as determined by skull condition) in first fall plumage were available, their average measurements did not vary from those of adults, nor did they differ from adults in plumage characters.

In studying geographic variation in color characters, individual variation, seasonal effect of wear, and "foxing" of museum specimens had to be weighed before geographic variation could be appraised. Post-mortem browning does occur and the changes are

most noticeable on the rectrices and remiges. Old specimens have lost the blue-gray tone that characterizes fresh specimens. While members of the family Paridae are prone to foxing to a greater degree than in many other families, I do not believe that Mountain Chickadees undergo such extreme post-mortem color change as Davis (1951:6) found in Brown Towhees. Some difficulties were presented where only old material of some populations was available and so had to be compared with new material of others. These cases are noted in the text. Capitalized color designations follow Ridgway (1912).

#### REVIEW OF PREVIOUS WORK

The species was first described as Parus montanus by Gambel (1843:259), based on a specimen taken about a day's journey west of Santa Fe, New Mexico. The name Parus montanus was shown by Ridgway (in A.O.U. Committee, 1886:335) to be preoccupied, and the name Parus gambeli was substituted. When Ridgway (1904:408) prepared the account for the Birds of North and Middle America no subspecies were known, although his measurements suggested that geographic variation did exist in the characters measured. The species was called Penthestes gambeli at that time. A few years later the race baileyae was described from southern California by Grinnell (1908: 29). Grinnell (1918) later undertook a systematic revision of the species and at that time described two additional races, invoensis from the desert mountains of eastern California and abbreviatus from northern California. The range of inyoensis was later found by Linsdale (1936:87) to extend throughout the Great Basin. The range of abbreviatus was extended by Oberholser (1919) to include Oregon, Washington, and central Idaho, and thence north to central western Alberta and northern British Columbia. However, van Rossem (1928) changed this concept of distribution when he described the subspecies grinnelli, with a range extending from east-central Oregon, eastern Washington and northern Idaho north through British Columbia. In the meantime Grinnell and Swarth (1926:163) described atratus from the Sierra San Pedro Mártir of Lower California.

A detailed picture of the distribution of the several races occurring in California was presented by Grinnell and Miller (1944:300–303). In the present review I have had essentially the same material that Grinnell and Miller so carefully worked over. As a result little information is added for the California region and it is corroborative of their findings. My major contribution has been to work out the picture of geographic variation in the populations farther east. In the course of this study the race wasatchensis was described (Behle, 1950), with a range covering central and southern Idaho, southwestern Wyoming and all of Utah except the mountains of the extreme eastern and western margins of the state.

# GEOGRAPHICALLY VARIABLE CHARACTERS

Color of dorsum.—This is one of the most variable characters of the species and in some cases serves as the principal basis for distinction between races. It is correlated to some extent with flank and side coloration. A well-marked north-south cline exists in this character in populations from the Cascade-Sierra Nevada southward through the mountains of southern California to the Sierra San Pedro Mártir of northern Lower California. The cline is toward increasing pigmentation or darker coloration to the south. Those examples representing the race abbreviatus are lightly gray. Those from the mountains of southern California representing baileyae are slightly darker, while those from the San Pedro Mártir called atratus are still darker, representing the extreme of dark gray coloration.

In addition there is a west-east cline which extends from the gray color of the atratus-baileyae-abbreviatus group to a light buff or tan color of inyoensis of the Great Basin, through a darker gray-green form, wasatchensis, which occurs just east of the Great Basin, to the brown of gambeli of the Rocky Mountain region. A slightly different transition from the gray coloration of coastal birds to the brown of Rocky Mountain birds is seen through eastern Washington and northern Idaho, where the race grinnelli represents a transitional stage.

Color of sides and flanks.—Accompanying the grayish dorsum of the coastal trio of races, abbreviatus-baileyae-atratus, the color of the sides and flanks is likewise gray and the same cline toward darker coloration to the south is manifest. In abbreviatus the flanks are tan-gray. In baileyae they are darker and dirty appearing but still tan-gray, while in atratus the flanks are still darker, more of a brown-gray. In the Rocky Mountain region (gambeli and grinnelli) the flanks are differently colored from the dorsum, being pinkish buff or cinnamomeous. Between these two areas a transition occurs so that the flanks of chickadees from the Great Basin and Utah mountains (inyoensis and wasatchensis) are buffy. In northwestern Nevada, however, the gray color of abbreviatus prevails. Farther north across eastern and central Washington a more erratic transition occurs. Some individuals with cinnamon colored flanks occur as far west as the east side of the Cascades. The blending of coastal gray and Rocky Mountain cinnamon is best seen in Okanogan County, Washington.

Amount of white on head.—The prominence of the superciliary stripe and its extent posteriorly, together with the amount of white in the frontal stripe of the head, are subject to great individual variation and also to some geographic variation. In the race atratus of northern Lower California the white is greatly reduced, being narrower and not extending so far posteriorly. This was brought out in the statement of Grinnell and Swarth (1926:163-164) made while comparing atratus and the neighboring race baileyae: "The white on the head of atratus is not only less in area occupied, but it is shallower; and birds in breeding plumage, when it is [further] reduced or effaced by wear, come to bear a curious resemblance about the head to Penthestes [= Parus] atricapillus." The amount of white seems to be fairly constant in the races baileyae, abbreviatus, grinnelli, gambeli and wasatchensis. The race inyoensis has the greatest amount of white, especially in examples from central northern Nevada.

Length of wing.—The races do not vary greatly in this character, as shown in figure 1. The greatest difference in wing length between races exists between gambeli and grinnelli.

Tail length.—In contrast to the wing, the tail length shows considerable variation between populations. The longest tail is found in wasatchensis of the Utah region. The race gambeli of the Rocky Mountains is next longest with inyoensis of the Great Basin a close third. The races of the coastal Sierra Nevada-Cascade Cordillera, abbreviatus, baileyae and atratus, are shorter tailed. Thus there is a west-east cline toward longer tails in the interior Rocky Mountain region. There is also a suggestion of a southward cline in the three coastal populations toward a longer tail, but differences in means are not statistically significant. The form grinnelli of the northern Idaho region is somewhat intermediate geographically between the Rocky Mountain and coastal races, but in tail length it is closer to the latter. Both sexes show the same differences between populations in tail length. It should be noted that whereas my tail measurement was the usual one from the point of insertion between the middle rectrices to the tip of the longest rectrix, Grinnell (1918:508) in his revision measured the tail from the base of the uropygium to the tip of the longest pair of rectrices. Hence the two sets of data are not directly comparable.

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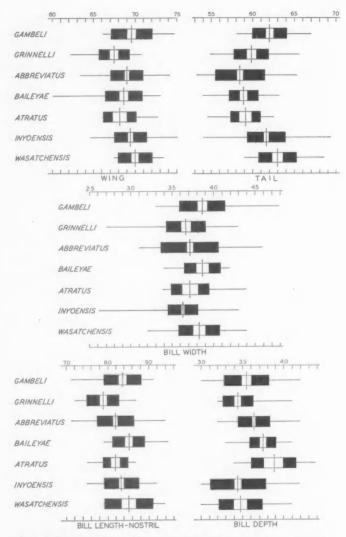


Fig. 1. Individual and geographic variation in several mensural characters of races of *Parus gambeli* based on adult males. Limits of variation shown by lengths of horizontal lines; means marked by vertical lines; dark rectangles represent standard deviation; light parts of rectangles, twice the standard error of the mean. Where the light areas do not overlap, differences in mean are statistically significant.

Wing-tail ratio.—Since tail length is more variable than wing length, the races differ in relative length of wing and tail. Comparison of the figures obtained by dividing the average wing length by the average tail length for each race is a better indication, perhaps, of differences between the various populations of chickadees in wing and tail lengths than that revealed by comparing absolute lengths of these characters. Wing-tail ratios for males of races are as follows: gambeli, 1.11; grinnelli, 1.12; abbreviatus, 1.18; baileyae, 1.16; atratus, 1.15; inyoensis, 1.12; wasatchensis, 1.10. While grinnelli is smaller than gambeli, the wing-tail ratio is essentially the same. With their short tails the coastal group of races, abbreviatus, baileyae, and atratus, show the largest wing-tail ratios in the order mentioned. Of special concern is the difference between grinnelli and abbreviatus. These two races have been considered by some writers to be indistinguishable, yet in wing-tail ratio there is a considerable difference. The interior races inyoensis and wasatchensis have proportions closer to gambeli and grinnelli than to the coastal group. The race wasatchensis has the smallest ratio of wing to tail. In this population the tail most nearly approaches the wing in length.

Bill length.—The bill of the race grinnelli is the shortest. Long-billed populations are gambeli, baileyae and wasatchensis. Intermediate are abbreviatus and inyoensis.

Depth of bill.—The Rocky Mountain and Great Basin races, namely gambeli, grinnelli, wasatchensis and inyoensis, are about the same in bill depth; the coastal races have deeper bills. Bill depth in the race abbreviatus is less than in baileyae and atratus. The latter has the deepest bill of all races. Thus in the three far western races there is a southward cline toward increasing bill depth at the base.

Bill width.—The bills of gambeli, baileyae, and wasatchensis are wider than those of the other races.

Bill types.—On the basis of the three bill dimensions of length, depth, and width it seems that the race grinnelli has the smallest bill all around; it is short, narrow, and shallow at the base. The bill of atratus is short but deep and of moderate width. That of baileyae is longer, deeper, and wider than its neighbor abbreviatus, although the two are generally similar in appearance. The races inyoensis and wasatchensis likewise are similar but are unlike the previous mentioned races in that they are longer and slenderer. The bill of gambeli differs decidedly from the last two and is more like that of grinnelli except it is larger and longer. Although racial differences in bill dimensions are slight, they are apparent in the averages. Yet Grinnell was partly right when he said (1918: 508) "neither depth of bill nor culmen is a practical index to degree of slenderness of bill. No ordinary measurement will suffice to indicate the facts...perceived by the eye."

Combining the measurable differences and visual impressions, it seems that three types of bill are represented in the species. In the Rocky Mountain area proper the bill is relatively short, stubby, thick at the base, and blunt; the northern population (grinnelli) is smaller, being shorter and thinner at the base. A second bill type occurs in the interior mountain region of Utah, Nevada, and eastern California, where the bill is long, slender, and tapers to a point. The more eastern population wasatchensis has a slightly longer and wider bill at the base than inyoensis. The third type is seen in the three races closest to the Pacific coast, namely atratus, baileyae and abbreviatus, where the bill is generally more massive, especially at the base, and, although variable among the three races as to length, it is quite unlike the long, tapering inyoensis-type bill. The bill of atratus resembles the remote gambeli far more than it does that of the intervening races inyoensis and wasatchensis.

Weight.—Samples of weight data among the various races are so inadequate that little can be judged of geographic variation in body weight. The indications are, however, that the races do not differ in average body weight. Large samples are available

for abbreviatus and inyoensis. Their average weights are very close, yet abbreviatus has a shorter tail. The small sample of grinnelli, which race shows shorter measurements in wing, tail, and bill than the other races, indicates no significant difference in average weight. Slight sexual difference in weight is suggested, which is probably correlated with slight difference in size; females average smaller.

Degree of variability of characters.—Comparing the coefficients of variation for the characters measured (fig. 2), the wing is the least variable, followed by the tail, length

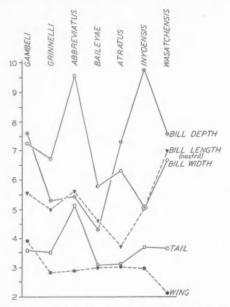


Fig. 2. Comparison of coefficients of variation of five mensural characters of adult males in the seven races of Parus gambeli.

of bill (from nostril), bill width, and bill depth. Wing and tail are considerably more conservative than the bill dimensions. In juncos (Miller, 1941:365), jays of the genus *Aphelocoma* (Pitelka, 1951:358), and Brown Towhees (Davis, 1951:92), the wing also is the least variable mensural character. Towhees and jays are similar in having the bill length more variable than bill depth. These are large-billed forms. Mountain chickadees are like juncos in having the bill depth more variable than bill length. The latter two are small-billed types.

## Parus gambeli gambeli Ridgway

Parus montanus (not of Baldenstein) Gambel (1843:259).

Parus gambeli Ridgway (in A.O.U. Check-list, 1886:335); new name for Parus montanus Gambel. Type locality.—About one day's journey west of Santa Fe, New Mexico.

Racial characters and comparisons.—This race is distinguished by the possession of a brown dorsum, cinnamomeous or pinkish buff flanks and sides, and a relatively short, stubby bill. As compared with neighboring races, it differs from wasatchensis in having a browner dorsum, shorter, stubbier bill, and the tail length averages slightly shorter. It has the same bill type as grinnelli but the

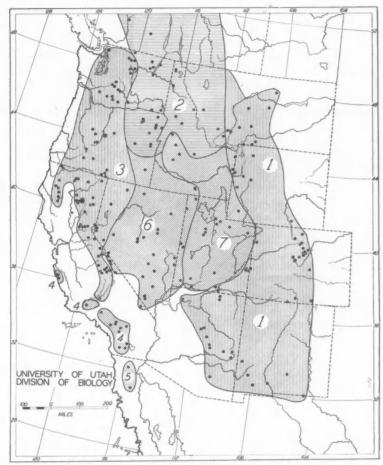


Fig. 3. The ranges of the races of Parus gambeli broadly outlined. Actual areas of occurrence within the ranges are discontinuous because these chickadees frequent only the coniferous forest in mountainous areas. 1, gambeli; 2, grinnelli; 3, abbreviatus; 4, baileyae; 5, atratus; 6, inyoensis; 7, wasatchensis.

bill averages slightly longer, wider, and deeper. Gambeli has a longer average wing and tail length than grinnelli. The principal difference from grinnelli, however, is the browner dorsum of gambeli.

Geographic distribution.—Rocky Mountain region from Montana (except the extreme western portion) south through Wyoming (except possibly the extreme southwestern portion) and Colorado to southern Arizona, New Mexico, and central western Texas (Davis Mountains). Occasionaly members wander outside their breeding range as indicated by a specimen from Smith Morehouse Creek, Weber River, Summit County, Utah, taken on October 11 within the breeding range of wasatchensis.

Specimen localities.—MONTANA: Gallatin County: Madison River, 2 (Sept.); near Hillsdale, 2 (Aug.); Jefferson River, 1 (Sept.); Mystic Lake, 1 (Sept.). Sweetgrass County: near head Big Tim-

ber Creek, Crazy Mountains, 1 (June). Park County: 2 mi. NE Cooke, 8500 feet, 1 (July). Judith Basin County: Dry Woolf Cr., Little Belt Mts., 20 mi. SW Stanford, 1 (Aug.). Carbon County: 2 mi. E Shriver, 6500 feet, 1 (July). Phillips County: Zortman, 2 (July). Fergus County: Hilger, 1 (Aug.). IDAHO: Fremont County: 17 mi. E, 4 mi. N Ashton, 1 (Aug.). WYOMING: Yellowstone National Park: Mammoth Hot Springs, 3 (Oct., Nov.); Teton County: Above Fish Creek, 7200 feet, Teton Pass, 2 (Sept.); 2 mi. SW Victor [, Idaho], 1 (July); Lincoln County: Head Dry Cr., 9200 feet, Salt River Mts., 1 (Aug.); Sublette County: "Near" Green River Lakes, 8000-8300 feet, 3 (Aug., Sept.); Carbon County: 25 mi. E, 10 mi. S Saratoga, 9800 feet, 4 (Sept.). Albany County: 7 mi. W, 4 mi. N Centennial, 11,000 feet, 1 (Sept.); Headquarters Park, 10,200 feet, Medicine Bow Mountains, 1 (June). UTAH: Summit County: Smith Morehouse Creek, Weber River, 1 (Oct.); Grand County: 15 mi. SE Moab, La Sal Mountains, 1 (April); San Juan County: Wilson Creek, La Sal Mountains, 1 (Oct.); 5 mi. NE La Sal P.O., 8000 feet, 2 (April); Navajo Mountain, 10,000 feet, 2 (June). Kane County: Kaiparowits Plateau, 2 (Aug.). COLORADO: Jackson County: Buffalo Park, 1 (Feb.). Larimer County: Medicine Bow Range, 2 (Aug.). Grand County: Granby, 4 (Oct., Nov.). Rio Blanco County: Rangeley, 1 (Oct.): Boulder County: Boulder, 3 (Feb., April); Longs Peak, 1 (July). Adams County: Henderson, 1 (Oct.). Jefferson County: Golden, 2 (Mar., Oct.); Morrison, 4 (Mar., Feb.); Arvada, 2 (May, Feb.); Turkey Creek, 1 (Oct.); Dome Rock, 1 (Oct.). Eagle County: Red Cliff, 1 (Dec.). Denver County: Clear Creek, Denver, 1 (Jan.). Lake County: Leadville, 2 (Mar.). Park County: Hall Valley, 2 (June, July). El Paso County: Manitou, 1 (Jan.). Montrose County: La Sal Mountains, 1 (May). Montezuma County: Ute Peak, 8500 feet, 1 (June). Conejos County: Sanford, 1 (Feb.); Osier, 10,000 feet, 1 (July). Las Animas County: Trinidad, 7 (Mar., Oct., Nov.). ARIZONA: Mohave County: Nixon Spring, 6250 feet, Mt. Trumbull, 1 (May). Coconino County: West side Agassiz Peak, 10,000 feet, 9 mi. NW Flagstaff, 1 (July); Deadman's Flat, 6400 feet, NE San Francisco Mountain, 9 (Sept.); Sawmill Springs, 7300 feet, 8 mi. SE Mormon Lake, 1 (July). Navajo County; Keet Siel Canyon, 7000 feet, 1 (Jan.); 8 mi. S White River, 6100 feet, 1 (April). Skeleton Mesa, 8000 feet, 20 mi. NW Kayenta, 1 (June). Pima County: Santa Catalina Mountains, 5 (Sept., Oct.). Gila County: Head of Workman Creek, Sierra Ancha, 1 (June); Aztec Peak, 6500 feet, Sierra Ancha, 1 (June). Greenlee County: Hannagan Meadow, 9500 feet, 2 (July). Apache County: Big Lake, 20 mi. S Springerville, 2 (June). NEW MEXICO: Catron County: Reserve, 12 (Oct.). Grant County: Pinos Altos, 1 (May). Luna County: Mimbres River, 2 (Mar.). Dona Ana County: Radium Springs [= Fort Selden], Rio Grande River, 2 (Mar.). Otero County: Cloudcroft, 1 (April). TEXAS: Culberson County: McKittrick Canyon, 8 mi. NE Guadalupe Peak, 5300 feet, 4 (Mar.).

Table 1

Measurements of Parus gambeli gambeli

		212000000000000000000000000000000000000		Same Same		
Dimension	Sex	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	8	73	66.0-74.7	69.57±0.29	2.50	3.59
	9	43	64.5-75.6	67.41±0.36	2.40	3.57
Tail	8	73	58.1-67.0	62.13±0.25	2.21	3.56
	9	43	56.6-67.5	60.72±0.37	2.45	4.04
Bill from	8	69	7.1- 9.1	8.35±0.05	0.46	5.56
nostril	2	43	7.6- 9.5	8.18±0.06	0.43	5.35
Depth of bill	8	59	3.0- 4.2	$3.55 \pm 0.03$	0.27	7.64
	9	38	3.0- 4.2	$3.45 \pm 0.04$	0.27	7.83
Bill width	8	70	3.3- 4.8	$3.87 \pm 0.03$	0.28	7.28
	9	43	3.2 - 4.8	$3.76 \pm 0.04$	0.32	8.61
Weight (grams)	8	17	10.5-13.5	11.87±0.18	0.74	6.27
	9	4	10.0-12.2	$10.78 \pm 0.33$	0.82	7.62

Geographic variation and intergradation.—Although gambeli occupies the whole Rocky Mountain region, it shows fair uniformity of color characters throughout its range. No constant color differences were detected between specimens at hand from Texas, Arizona, and New Mexico and the Colorado-Wyoming-Montana area. However, intergradation occurs where the range of gambeli impinges upon that of the races wasatchensis and grinnelli. Fresh fall specimens from the San Francisco Mountains of northern Arizona and a few worn examples from Mount Trumbull, Navajo

Mountains, and the Kaiparowits Plateau, all of which localities are near the Utah-Arizona border, are intermediate between wasatchensis and gambeli but closer to the latter. Incidentally, van Rossem (1928:105) assumed that birds from the San Francisco Mountains were typical of gambeli. To me they seem to be intergrades. Examples from the La Sal Mountains of southeastern Utah, almost on the Colorado border, also are intergrades and again closer to gambeli. Presumably intergradation between these two races continues to the north, but there is no material to demonstrate this except that from near the northeastern part of the range of wasatchensis. Specimens from near Green River Lakes, Sublette County, near Teton Pass, Teton County, and the Head of Dry Creek, Salt River Mountains, Lincoln County, all in western Wyoming, and others from 17 miles east and 4 miles north of Ashton in nearby Idaho show the attenuated bill of wasatchensis; but their coloration is closer to gambeli, under which they have been listed.

Apparently the ranges of gambeli and grinnelli come together in southwestern Montana. Whereas examples from Gallatin, Sweetgrass and Park counties are closest to gambeli, those from the Dillon area and the Ruby Mountains are closest to grinnelli. A specimen from Dry Wolf Creek, Little Belt Mountain, 20 miles southwest of Stanford, also is intermediate but closer to gambeli.

## Parus gambeli grinnelli (van Rossem)

Penthestes gambeli grinnelli van Rossem (1928:104).

Type locality.-Priest Lake, 2450 feet, Bonner County, Idaho.

Racial characters and comparisons.—Distinctive characters of this race are a short, stubby bill, short wing and tail, and grayish-green, less brownish dorsum. As compared with gambeli it has the same bill type and wing-tail ratio but is smaller throughout. It differs in addition in being darker (gray-green, less brown) on the dorsum and having lighter flanks and sides. In describing grinnelli, van Rossem (1928:104) commented that in relative darkness of tone, grinnelli bears much the same relation to gambeli as baileyae does to abbreviatus. Grinnelli is distinguished from abbreviatus by shorter wing length and proportionately longer tail as well as darker, greener, less grayish dorsum. From wasatchensis, grinnelli differs in markedly shorter, stubbier bill and darker, gray-green coloration. There is greater variation in flank color in grinnelli than in other races.

Geographic distribution.—Extreme western Alberta (Smoky River, Henry House, fide Hellmayr, 1934:75) and northern British Columbia west of the Rocky Mountains (Doch-da-on Creek on the Upper Stikine River) south through eastern Washington, northern Idaho, and extreme western Montana to northeastern Oregon and central Idaho. Vagrants may occur outside the breeding range, although two supposed records had best be discounted. Van Rossem (1928:104) referred a specimen from Tacoma, Pierce County, Washington, taken on December 21, and one from Hope, British Columbia, to this race as wanderers west of the Cascades. However, the Tacoma specimen seems to me to be an example of abbreviatus which has become darker through adventitious coloration, and according to Brooks and Swarth (1925:117) the Hope record is based on a manuscript reference.

Specimen localities.—BRITISH COLUMBIA: Atlin, 1 (June); Mountain at 3000 feet, above Dochda-on Creek, Stikine River, 3 (July); Nine-mile Mountain, 4000 feet, northeast Hazelton, 1 (July); 8 mi. N Clearwater P.O., 1 (June); Okanagan Landing, 2 (Sept.); Okanagan, 5 (Feb.); Spences Bridge, 1 (Mar.). WASHINGTON: Okanogan County: Aeneas, 8 (Feb.); Republic, 4 (Nov.); Bauerman Ridge, 6 (Sept.). Benton County: Prosser, 2 (Oct.). Asotin County: Anatone, 1 (June). Columbia County: 1 mi. W Stayawhile Spring, 5300 feet, 1 (July). Yakima County: Toppenish Ridge, 3400 feet, 10 mi. SW Fort Simeol, Yakima Indian Reservation, 1 (Sept.). Stevens County: Marcus, 1 (Sept.); Whatcom County: Bellingham, 1 (Nov.). Spokane County: Fort Spokane, 1 (Sept.). Ferry County: Curlew Lake, 5 (Nov.). oregon: Umatilla County: Meacham, 1 (July). Union County: Kamela, 1 (June). Wallowa County: Wallowa Lake, 4000 feet, 1 (April). Baker County: 11 mi. E Unity, 1 (Dec.); Anthony, 1 (Oct.); North Pine Creek, 3000 feet, 1 (June). Malheur County: Willow Creek, Ironside, 1 (Dec.). IDAHO: Kootenai County: Coeur d' Alene, 7 (Apr., Sept., Feb.). Bonner County: Coolin, 1 (Sept.); Priest Lake, 1 (Aug.); Lost Creek, 6500 feet, 1 Sept.); Hunt Creek, 3200 feet, 3 (July). Elmore County: Horseheaven Creek, 6000 feet, 2 (Dec.); Hunter Creek, 6000 feet, 1 (Dec.); North Fork Boise River, 6000 feet, 1 (Dec.). Idaho County: 4 mi. SW Selway Falls, 5500 feet, 1 (Sept.); Beaver Ridge, 81/2 mi. SE Lola Pass, 7000 feet, 1 (July); Castle Creek R.S., South Fork Clearwater River, 1800 feet, 1 (July). Latah County: Bald Mountain, 2 (Sept.). Custer County: Dickey, 2 (June). Adams County: Summit Smith Mountain, 7500 feet, 1 (July). MONTANA: Missoula County: Lolo Creek, 6½ mi. W Lolo, 3470 feet, 2 (May). Beaverhead County: Birch Creek, 18 mi. NW Dillon, 7100 feet, 1 (July). Madison County: 12 mi. SW Alder, Ruby Mountains, 1 (Aug.).

Dickinson (1953:170) in reporting on the McCabe collection from the Fraser River drainage area of British Columbia lists specimens under *grinnelli* from the following localities: Anahim Lake, Birch Island, Chezacut, Clearwater, Hotnarko River, Indianpoint Lake, Lytton, 100 Mile House, Quesnel, Redstone, Watson Lake.

Geographic variation and intergradation.—The presumed center of differentiation, or at least the area from which typical specimens come, covers northern Idaho and adjacent areas in extreme eastern Washington, southeastern British Columbia, and northwestern Montana. Fringing this center are areas of intergradation with surrounding races. That between grinnelli and gambeli in southwestern Montana has been noted in the account of gambeli. There is an area of intergradation between grinnelli and wasatchensis in central Idaho (see account of wasatchensis). Either wasatchensis or inyoensis is involved along with abbreviatus in a confusing area of blending in the Blue Mountain region of Wallowa, Baker, and Grand counties in northeastern Oregon and extreme southeastern Washington. I have referred these heterogeneous specimens to grinnelli because their dorsal coloration is darker than that of the other races mentioned and, therefore, most like grinnelli. However, the specimens are for the most part worn and frayed. The bills are variable; some are small and stubby as in grinnelli but most are long and tapering as in inyoensis and wasatchensis. Flank color is more like abbreviatus.

Specimens showing this mixture of characters are as follows: OREGON: Wallowa County: 16 mi. S, 3 mi. E Lostine, 5500 feet, 9 (July); 25 miles north Enterprise at Sled Springs, 4600 feet, 3 (April). Grant County: north fork Malheur River, 21 mi. SE Prairie City, 5000 feet, 9 (July); Summit Creek, 6700 feet, 7 mi. E Austin, 2 juveniles (July). Union County: Grande Ronde Lake, 7100 feet, 1 (July). WASHINGTON: Columbia County: Blue Mountains, 5000 feet, 21 mi. SE Dayton, 2 (June).

When Gabrielson and Jewett (1940:434) extended the range of grinnelli into southeastern Oregon they assigned their birds from the Steens Mountains and Rome to grinnelli. These birds may also represent this intermediate population although I have assigned a fall specimen from Rome to invoensis.

Table 2
Measurements of Parus gambeli grinnelli

		MACGGGICILL	HES OI A WINS S	Consocus Brancos		
Dimension	Sex	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	3	47	62.2-70.7	67.40±0.27	1.86	2.75
	9	25	60.4-69.9	64.95±0.45	2.25	3.46
Tail	8	47	54.4-65.2	59.85±0.30	2.12	3.54
	9	25	53.9-60.9	57.64±0.33	1.67	2.89
Bill from	8	47	7.2 - 8.7	$7.88 \pm 0.05$	0.39	5.01
nostril	9	25	7.0- 8.5	7.80±0.08	0.40	5.21
Depth of bill	8	39	3.2- 4.1	3.45±0.02	0.18	5.33
	9	21	2.8- 4.0	$3.50 \pm 0.07$	0.32	9.21
Bill width	8	46	2.7- 4.3	$3.67 \pm 0.03$	0.24	6.74
	9	25	3.2 - 4.3	$3.60 \pm 0.05$	0.25	6.94
Weight (grams)	8	9	9.0-13.0	$11.48 \pm 0.44$	1.32	11.60
	9	4	10.7-12.0	$11.25 \pm 0.30$	0.61	5.45

Although Gabrielson and Jewett (loc. cit.) refer to grinnelli as a somewhat poorly differentiated form, they state that they had fairly typical specimens of that race from Wallowa, Baker, Grant, and Crook counties, Oregon. According to the present writer's concept, specimens from Wallowa and Baker counties would be atypical since they are intergrades closest to grinnelli, while those from Grant and Crook counties also are intergrades, those from Crook County at least being closer to abbreviatus. When van Rossem (1928:104) described grinnelli, he noted this intergradational area between grinnelli and abbreviatus in east-central Oregon. He referred an atypical specimen from Anthony, Baker County, to grinnelli but three from Prineville, Crook County, to abbreviatus, with which disposition I agree.

The broad belt of intergradation between abbreviatus and grinnelli extends north into Washington through Chelan and Okanagan counties. I have somewhat arbitrarily placed specimens from longitude 120° and westward with abbreviatus and have listed the intermediate specimens in that

racial account. However, five September specimens in that intermediate zone from Bauerman Ridge, located east of Cathedral Peak near the Canadian boundary in northwestern Okanagan County, have cinnamon flanks and seem closer to grinnelli. Perhaps it was this broad zone of intergradation that prompted Jewett, Taylor, Shaw, and Aldrich (1953:479) to comment: "Although birds from northern Idaho and northern Oregon and northward are minutely smaller and darker than abbreviatus of northern California, southern Oregon, and western Nevada, there is far too great an overlapping to identify satisfactorily a large percentage of individuals. Therefore, the northern race, grinnelli, appears not to be recognizable."

## Parus gambeli abbreviatus (Grinnell)

Penthestes gambeli abbreviatus Grinnell (1918:510).

 $Type\ locality$ .—Horse Creek, near [ = 7 miles northeast of] Seiad P.O., [on south slope of] Siskiyou Mountains, Siskiyou County, California.

Racial characters and comparisons.—Gray coloration, intermediate-sized bill and short tail characterize this race. As compared with surrounding races, abbreviatus is closest to baileyae, having prevailing gray coloration, heavy bill, and similar proportions of wing and tail, but it differs in being lighter and having a smaller bill both as to length and size at the base. Abbreviatus differs from grinnelli in having a grayer, less greenish dorsum; the tail is relatively shorter and the bill is larger and longer. It is distinguished from inyoensis by its grayer and darker dorsal coloration, shorter and heavier bill, and relatively shorter tail. Grinnell (1918:510) indicated that the tone of color of the sides, flanks, and back of abbreviatus is, in fresh plumage, the same as in inyoensis, namely Cartridge Buff, though not quite so pale. It seems to me that the whole appearance of abbreviatus is generally grayer. Only in some extreme individuals or in birds from intergrading regions does the buff color of the flank occur which shows an approach to inyoensis.

Geographic distribution.—Interior mountain ranges of central Washington, west through the Cascades and south through central and southwestern Oregon to northwestern Nevada and eastern California (exclusive of Inyo district) as far south as the Piute Mountains, Kern County. In the coast ranges of northwestern California the species occurs in the Siskiyou and Trinity mountains and southward in the higher parts of the inner coast ranges to Mount Sanhedrin, Mendocino County, and Snow Mountain, Colusa County. The species only occurs in the humid coast belt as a straggler (fide Grinnell and Miller (1944:300)).

When Grinnell (1918:510) described the race abbreviatus, he included in its range the higher mountains of central and northern California and northwestern Nevada. He presumed that it extended into southern Oregon. Oberholser (1919:424) restated the range on the basis of material in the Biological Survey collection to include in addition, Oregon, Washington, central Idaho, southwestern Alberta, and British Columbia. Swarth (1922:297, 1924:368, 1926:142) initially assigned his specimens from British Columbia to the race abbreviatus, but with van Rossem's description of grinnelli (1928:104) it developed that the birds of British Columbia belonged to the latter race. If abbreviatus occurs in British Columbia at all, it is probably confined to the extreme southwestern corner.

Specimen localities.-washington: Pierce County: east slope Mt. Rainier, 1 (Aug.). Yakima County: Pine Grass Ridge, near Signal Peak, 4000 feet, 1 (July); Klickitat Meadows, 2 (Sept.); Reynolds Creek, Cowichee, 3000 feet, 2 (May); near Potato Hill, 4500 feet, 15 mi. N Goldendale, Yakima Indian Reservation, 1 (Aug.); head of Hindos Creek, 6500 feet, Mt. Aix, 1 (Sept.); 3 mi. NE at Goose Prairie, 5000 feet, Bumping Lake, 2 (Aug.); Foundation Ridge, Ahtanum, 4000 feet, 1 (May); Mt. Adams, 2 (Oct.). Skamania County: Mt. St. Helens, 2 (June), 1 (Sept.). OREGON: Wheeler County: 11 mi. W, 7 mi. S Mitchell, 4850 feet, 8 (June). Tillamook County: Happy Camp, Netarts, 1 (Dec.). Crook County: 6 mi. E, 3 mi. N Wildcat Mountain, 4700 feet, 1 (June); Ochoco R.S., 1 (June). Deschutes County: West Silver Creek, 4650 feet, 10 mi. SW Silverlake, 1 (Sept.); 7 mi. NW Sisters, 3300 feet, 1 (June); 4 mi. N, 9 mi. W Sisters, 4000 feet, 5 (June); 1 mi. SE Paulina Lake, 4 (June); 3 mi. W Paulina Lake, 5700 feet, 3 (June); Tumalo Creek, 11-15 mi. W Bend, 6 (June); Swampy Lakes, 13 mi. W and 3 mi. S Bend, 4 (June). Douglas County: 5 mi. S Mt. Thielson, 2 (June), Lake County: Drews Creek, 1 (June); Barley Camp, Warner Mountain, 17 mi. SW Adel, 1 (June); north base Crook Peak, Warner Mountains, 1 (June); Lakeview, 1 (Oct.); 2 mi. E Lakeview, 5200 feet, 1 (May). Klamath County: Fort Klamath, 1 (Nov.), 1 (Sept.), 1 (Dec.). NEVADA: Humboldt County: near Alder Creek Lake, Pine Forest Mountains, 2 (July); west side Pine Forest

Mountains, 2 (July). Washoe County: Galena Creek, 7000-7500 feet, 8 (May), 3 (Oct.); 6 mi. N Incline, 9500 feet, 2 (May); ¼ mi. SE Incline, 6300 feet, 1 (April); east side Granite Mountain. 1 (Oct.), Churchill County: 4 mi. SW Fallon, 4000 feet, 3 (Mar.), 1 (Oct.), Lyon County: West Walker River, 4900 feet, 1 (Mar.). Mineral County: 2 mi. SW Pine Grove, 2 (June). CALIFORNIA: Humboldt County: Horse Mountain, 4700 feet, 2 (June); Brannan Mountain, 3500 feet, 2 (Sept.); South Fork Mountain, 5700 feet, nr. Blake Lookout, 2 (June-July), Siskivou County: Seiad Val. P.O., Horse Creek, Siskiyou Mountains, 10 (Nov. to Feb.); Kangaroo Creek, 2 (Aug.); Jackson Lake, 5900 feet, 5 (June); South Fork Salmon River, 5000 feet, 1 (July); T. H. Benton Estate, Butte Creek, 8 (Aug.); Grass Lake, 5000 feet, 2 (May); Mt. Shasta, 1 (July). Trinity County: Head Grizzley Creek, 6000 feet, 3 (July); 8 mi. NE Hyampom, 2900 feet, 2 (Sept.); 2 mi. E Hayfork, 2400 feet, 1 (June); Red Mt., 5300 feet, 14 mi. S Hayfork, 1 (Sept.), White Rock Ranger Station, 4800 feet, and 4 mi. E, 4 (May); Miller's Spring, 5000 feet, South Fork Mountain, 2 (June); The Racetrack, 5500 feet, South Fork Mountain, 2 (June); 4 mi. N, 1 mi. W Norse Butte, 5000 feet, South Fork Mountain, 2 (Aug.); Reilley's Ranch, 3000 feet, South Fork Mountain, 9 (Mar., Apr., May); South Fork Mountain, 4 mi. N Mad River Rock, 4200 feet, 1 (Jan.); Divide, 12 mi. N North Yolla Bolly Mountain, 4400 feet, 4 (May); 1 mi. SW North Yolla Bolly Mountain, 1 (Aug.). Modoc County: 8 mi. N. 13 mi. W Canby, 4700 feet, 1 (May); Sugar Hill, 5500 feet, 4 (May); Parker Creek, 5500 feet, Warner Mts., 10 (June-July); Shield's Creek, 5000 feet, 1 (June). Lassen County: 4 mi. SW McDonald Peak, 5300 feet, 1 (Oct.); 5 mi. N Fredonyer Peak, 1 (Oct.); 4 mi. W, 2 mi. N Susanville, 5000 feet, 3 (June); 8 mi. NE Susanville, 4800 feet, 1 (Jan.). Shasta County: Harrison Gulch, 2600 feet, 1 (Feb.); Manzanita Lake, 6000 feet, 3 (June). Tehama County: 11 mi. E Payne's Creek Post Office, 3500 feet, 1 (Dec.); Payne Creek, 600 feet, 2 (Dec.); Mineral, 4900 feet, 2 (May, Dec.); Lyman's, 3300 feet, 4 mi. NW Lyonsville, 1 (June). Butte County: Stanwood, 1 (June). Plumas County: Willow Lake, 5600 feet, 1 (July); Meadow Valley, 1 (June). Nevada County: 1 mi. W Nevada City, 1 (Oct.); Grass Valley, 2 (Oct.); Boca Spring, 6000 feet, 2 (May); Sage Hen Creek, 6500 feet, 3 (Nov.). Placer County: Tahoe Valley, 2 (Sept.); Cisco, 13 (June, Sept., Oct.); Blue Canyon, 5000 feet, 10 (Oct.); Dutch Flat, 3400 feet, 1 (Aug.). El Dorado County: Kyburz Station, 1 (Aug.); Slippery Ford [= Kyburz Station] 1 (June). Alpine County: 4 mi. W Lookout Peak, 7900 feet, 1 (Sept.); 3/4 mi. S Woodford, 5500 feet, 1 (May). Mariposa County: Merced Grove Big Trees, 1 (June); Gentry's, 5800 feet, Big Oak Flat Road, Yosemite Park, 1 (Oct.); Cascades, Coulterville Road, Yosemite Park, 4500 feet, 1 (Nov.); Dudley, 3000 feet, 2 (July); Yosemite Valley, 4000 feet, 1 (Dec.); Eagle Peak Trail, 6800 feet, 1 (Dec.); Yosemite Falls Trail, 4000 feet, 2 (Dec.); Porcupine Flat, 8100 feet, 2 (June); 1 mi. E Merced Lake, 7500 feet, Yosemite Park, 1 (Aug.); East Fork, Indian Canyon, 7300 feet, 1 (June). Mono County: 7500 feet, on William's Butte, 1 (Sept.); Warren Fork of Leevining Creek, 9200 feet, 1 (Sept.); Sweetwater Canyon, 7900 feet, Sweetwater Mts., 2 (June); 7300 feet, nr. Convict Creek, Long Valley, 1 (July). Fresno County: Shaver R.S., 5300 feet, 2 (July); Bullfrog Lake, 10,600 feet, 6 (Sept.). Tulare County: near Twin Lakes, 2 (Aug.); Redwood Mt., 6500 feet, 10 mi. E Badger, 1 (June); Piute Mt., 9300 feet, 30 mi. S Bishop, 1 (July); Little Onion Valley, Sierra Nevada, 7500 feet, 1 (May); Onion Valley, 8500 feet, Kearsarge Pass, 1 (June); Whitney Creek, 11,000 feet, Sierra Nevada, 3 (Aug.); Silliman Crest, Sequoia Park, 1 (June); Whitnev Meadow, 9800 feet, Sierra Nevada, 5 (Aug.); Little Lake, Kern Canyon, 2 (July); Ouaking Aspen Meadow, 7500 feet, 1 (July); near Olancha Peak, Sierra Nevada, 10,000 feet, 1 (Aug.); Trout Creek and 4 mi. N Trout Creek, 7500 feet, 5 (July); Cannell Meadow, 7500 feet, 1 (July); Song Meadow, 7700 feet, 1 (July); Taylor Meadow, 7000 feet, 3 (July). Kern County: Kiavah Mt., 7000 feet, near Walker Pass, 1 (June); French Gulch and Meadow, 7500 feet, Piute Mts., 2 (Oct.). Inyo County: Cottonwood Lakes, 11,000 feet, Sierra Nevada, 6 (Aug.-Sept.); 21/2 mi. S and 6 to 81/2 mi. W Big Pine, 9000 feet, 7 (June); Independence, 3900 feet, 1 (May); Onion Valley, 9000 feet, 71/2 mi. W 2 mi. S Independence, 3 (June); east side Independence Peak, 8500 feet, 3 (May); 6 mi. W 3¼ mi. S Lone Pine, 6300 feet, 1 (May); Lone Pine Creek, 8200 feet, 91/2 mi. W, 11/4 mi. S Lone Pine, 2 (May); Lone Pine Creek, 9500 feet, 21/2 mi. E Mt. Whitney, 1 (May); 4 mi. S, 4 mi. W Olancha, 6500 feet, 1 (May); 13/4 mi. N, 1 mi. W Round Mt., 8600 feet, 1 (May).

Geographic variation and intergradation.—In Washington and Oregon, abbreviatus occurs in typical form in the Cascade Mountains. In the interior mountains to the east a zone of contact occurs with grinnelli, as noted in the account of that race. On the basis of the aggregate of characters, I regard

the following atypical specimens from this intergrading area in Washington as closer to abbreviatus: Whatcom County: Barron and 5 mi. W Barron, 2 (Aug.). Okanogan County: Lost River, 1 (June); Mazama, 2 (April); Twisp, 1 (April). Chelan County: Lucerne, 1 (July); Entiat River, 20 mi. from mouth, 1 (July); Tyee Peak, 5000 feet, 1 (July). The following intergrades from Oregon are also closer to abbreviatus: Crook County: Maury Mountains, 1 (June); 4 mi. SW Prineville, 3300 feet, 1 (June); 7 mi. W Prineville, 1 (July).

In the Sierra Nevada of California abbreviatus also occurs in typical form as far south as Mount Whitney, where the population starts to intergrade with baileyae. Chickadees from as far south as the Piute Mountains, Kern County, are, however, still referable to abbreviatus.

Table 3

Measurements of Parus gambeli abbreviatus

	Transfer of a min Position months and									
Dimension	Sex	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation				
Wing	8	220	63.3-74.2	$69.06 \pm 0.12$	1.96	2.84				
	9	88	62.2-70.7	65.97±0.20	1.88	2.85				
Tail	8	221	53.2-65.4	58.51±0.20	3.03	5.18				
	9	86	52.0-61.9	55.85±0.27	2.54	4.55				
Bill from	8	218	7.1- 9.4	8.18±0.03	0.45	5.61				
nostril	2	85	7.2- 9.1	8.07±0.04	0.41	5.16				
Depth of bill	8	204	3.2 - 4.2	$3.64 \pm 0.01$	0.19	5.46				
	9	79	3.1 - 4.5	$3.58 \pm 0.29$	0.26	7.32				
Bill width	8	219	3.1- 4.6	$3.72 \pm 0.02$	0.35	9.59				
	9	84	3.0- 4.2	$3.67 \pm 0.02$	0.25	6.91				
Weight (grams)	8	113	10.0-14.3	11.68±0.07	0.78	6.71				
	2	48	9.4-14.5	$11.13 \pm 0.16$	1.11	9.97				

Intergradation with inyoensis occurs in the Mono Lake area of central eastern California. This is discussed in the account of the latter race. Another possible area of contact between inyoensis and abbreviatus is in northeastern California, where some fall examples from eastern Lassen County have flanks that are buff rather than gray, which is an inyoensis character. Four January specimens from near Susanville are darker than most other examples of abbreviatus. These specimens may be vagrants or it may be that this area is one of great variability in the population. Specimens from the Pine Forest Mountains, Humboldt County, Nevada, to the east are referable to abbreviatus. A specimen from Minidoka, in central southern Idaho, taken March 25, 1915, is either a vagrant of abbreviatus well east of its range or an extreme variant of grinnelli that resembles abbreviatus.

# Parus gambeli baileyae Grinnell

Parus gambeli baileyae Grinnell (1908:29).

Type locality.—Mount Wilson, 5500 feet, San Gabriel Mountains, near Pasadena, Los Angeles County, California.

Racial characters and comparisons.—Characterized by a distinctly plumbeous color on the sides, flanks, and dorsum, heavy bill, especially at the base, and a short tail, the tail being nearly as short as in abbreviatus. The color of the dorsum is close to Deep Grayish Olive or Mouse Gray. The flank color is Smoke Gray. This race can be distinguished from abbreviatus by its darker, more plumbeous appearance and longer, larger, and heavier bill; the bill is especially thick at the base. As compared with invoensis, baileyae is considerably darker and more plumbeous, has a shorter tail, and the bill is larger and heavier. It differs from atratus in lighter coloration and more extensive white on the head.

Geographic distribution.—Baileyae has a discontinuous distribution in the higher mountains of southern California from the Santa Lucia Mountains of Monterey County and the Tehachapi Mountains of Kern County south through the San Gabriel, Santa Ana, San Bernardino, Little San Bernardino, and Jacinto, and Santa Rosa mountains to the Cuyamaca and Laguna mountains in San Diego County. Altitudinal range for nesting birds is from 3000 to 10,600 feet. In winter chickadees of this race are known to occur in the lower valleys at the bases of the mountains, having been recorded from Pasadena and in the desert along the Mohave River at Victorville.

Specimen localities .- CALIFORNIA: Monterey County: Santa Lucia Pk., 1 (May); Nacimiento

River, 2000 feet, Santa Lucia Mts., 1 (Aug.). Ventura County: Mt. Pinos, 8500 feet, 2 (July). Los Angeles County: Pasadena, 3 (Sept.-Oct.); Arroyo Seco Canyon, 1 (Dec.); Mt. Wilson, San Gabriel Mts., 17 (May, Oct., Nov., Dec., Feb.); Buckhorn Canyon, San Gabriel Mts., 2 (July); Old Mt. Wilson Trail, 4000 feet, San Gabriel Mts. near Pasadena, 4 (Mar.-Nov.). San Bernardino County: Hog Canyon, Yucaipa, 1 (Jan.); Cajon Canyon, 1 (Dec.); S side Bear Lake, 1 (June); Fawnskin Meadows, Bear Lake, 1 (June); Saragossa Springs, 7500 feet, San Bernardino Mts., 1 (Aug.); Bluff Lake, 7500 feet, San Bernardino Mts., 1 (July); Seven Oaks, 5100 feet, San Bernardino Mts., 1 (July); Fish Creek, 6500 feet, San Bernardino Mts., 1 (July); Dry Lake, 9000 feet, San Bernardino Mts., 1 (June); San Bernardino Mts., 5 (May, June); Santa Ana River, 5500 feet, San Bernardino Mts., 3 (July, Aug.); South Fork Santa Ana River, 7500 feet, 2 (Aug.); San Gordonio Peak, 10,000 feet, San Bernardino Mts., 3 (June, July); Victorville, Mohave River, 2 (Dec.). Riverside County: Schain's Ranch, San Jacinto Mts., 4 (June); Fuller's Mill, San Jacinto Mts., 2 (June); Trail between Fuller's Mill and Idyllwild, San Jacinto Mts., 1 (July); Canyon east of Round Valley, 8500 feet, and Round Valley, 9000 feet, San Jacinto Mts., 2 (July); Strawberry Valley, 6000 feet, San Jacinto Mts., 2 (July); Thomas Mt., 6800 feet, San Jacinto Mts., 1 (Aug.); Garnet Queen Mine, 6000 feet, Santa Rosa Mts., 5 (June, July); Santa Rosa Peak, 7500 feet, Santa Rosa Mts., 3 (June); Stubby Spring and 2 mi. N 4500-4750 feet, Little San Bernardino Mts., 8 (Sept., Dec.); Split Rock Tank, 4100 feet, Little San Bernardino Mts., 3 (Oct.); Lower Covington Flat, 5600 feet, 2 (Aug.). San Diego County: Julian, 1 (July); Cuyamaca Mts., 6 (Aug., Sept.); Morris Ranch, 5500 feet, Laguna Mts., 2 (Jan.).

Table 4

Measurements of Parus gambeli bailevae

		Measureme	nts of Farus !	gamben baneyae		
Dimension	Sex	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	8	58	60.0-73.0	68.7 ±0.29	2.28	3.00
	2	37	63.4-68.7	$66.08 \pm 0.20$	1.22	1.84
Tail	8	56	54.0-63.3	58.93 ± 0.24	1.90	3.06
	Q	36	54.0-60.3	56.62±0.26	1.57	2.78
Bill from	8	56	7.9- 9.5	8.51±0.05	0.39	4.65
nostril	2	33	6.3- 9.2	8.30±0.09	0.52	6.34
Depth of bill	8	54	3.3- 4.1	$3.75 \pm 0.02$	0.16	4.34
	2	33	3.0- 4.0	$3.58 \pm 0.03$	0.21	6.00
Bill width	8	55	3.4- 4.2	$3.87 \pm 0.04$	0.22	5.78
	9	33	3.2- 4.2	$3.74 \pm 0.04$	0.24	6.54
Weight (grams)	8	1	12.1			
	9	2	10.7-11.2			

Geographic variation and intergradation.—While the distribution of this race is discontinuous, there appear to be no significant differences among the populations from different mountain ranges. The only intergradation with a contiguous race occurs in the southern Sierra Nevada where baileyae merges with abbreviatus. Concerning this Grinnell (1918:512) remarked "Abundant material at hand from that portion of the Sierra Nevada immediately south of Mount Whitney shows complete transition from Penthestes gambeli baileyae to P.g. abbreviatus; in fact, many of the specimens can only be placed arbitrarily in one category or the other." As noted in the account of abbreviatus, Piute Mountains marks the intermediate point in this transition, specimens from south of that point being judged closest to baileyae.

#### Parus gambeli atratus (Grinnell and Swarth)

Penthestes gambeli atratus Grinnell and Swarth (1926:163).

Type locality.--La Grulla, 7200 feet, Sierra San Pedro Mártir, Lower California, México.

Racial characters and comparisons.—The race atratus is distinguished by its dark, slaty coloration and reduced amount of white in the superciliary and frontal region. The slate color is most apparent on the rectrices and remiges, especially in birds in fresh fall plumage. The dorsal coloration is Dark Olive and the flank is Light Grayish Olive. Since this form occurs at the southernmost part of the range of the species, it is close geographically only to the race baileyae, from which it differs in darker coloration, reduced white in the head region, and slightly longer average tail length.

Geographic distribution.—Sierra San Pedro Mártir and the Sierra Juárez of northern Lower California. In winter these chickadees drop down to lower levels (see Grinnell, 1928:223).

Specimen localities.—Lower California: Vallecitos, 8500 feet, San Pedro Mártir Mts., 8 (May, June); Concepción, 6000 feet, San Pedro Mártir Mts., 1 (Nov.); La Grulla, 7200 feet, San Pedro Mártir Mts., 14 (May, Oct.); Laguna Hanson, 5200 feet, Sierra Juárez, 14 (Oct.); Los Pozos, 4200 feet, Sierra Juárez, 1 (Nov.); El Valle de la Trinidad, 2500 feet, 2 (Nov., Dec.).

Table 5
Measurements of Parus gambeli atratus

				9		
Dimension	Sex	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	8	21	66.1-72.6	68.24±0.45	2.08	3.05
	Q	20	63.0-68.7	66.52±0.65	2.94	4.27
Tail	3	21	54.6-62.6	59.20±0.40	1.84	3.11
	2	19	53.0-60.9	58.28±0.47	2.09	3.58
Bill from	3	20	7.5- 8.7	8.18±0.06	0.30	3.73
nostril	\$	20	7.7- 9.0	$8.38 \pm 0.08$	0.37	4.41
Depth of bill	8	20	3.4- 4.4	$3.88 \pm 0.06$	0.27	7.24
	\$	20	3.5- 4.5	3.76±0.05	0.24	6.38
Bill width	8	20	3.4- 4.4	3.72±0.05	0.23	6.34
	Q	20	3.3- 4.3	3.76±0.06	0.26	7.18
Weight (grams)	8	19	10.0-12.2	11.23±0.14	0.62	5.62
	2	20	8.2-12.1	10.45±0.18	0.83	7.99

Geographic variation and intergradation.—The race atratus is isolated from its only neighboring race, baileyae, to the north but the hiatus is not appreciably greater than that between some of the populations in the discontinuous range of the wider-ranging, more northern race. Since baileyae is darker than abbreviatus and atratus is darker than baileyae, atratus occupies a terminal position in a north-south cline toward darker coloration. This is not peculiar to chickadees, for Grinnell and Swarth (1926:164) point out that many other geographically variable birds from this same region have their dark colors accentuated. This suggests that some environmental effect in the Sierra San Pedro Mártir makes for darker pigmentation. For a further discussion of this center of differentiation see Grinnell (1928:8).

# Parus gambeli inyoensis (Grinnell)

Penthestes gambeli invoensis Grinnell (1918:509).

Type locality.—Three miles east of Jackass Spring, 6200 feet, Panamint Mountains, Inyo County, California.

Racial characters and comparisons.—Characterized by light buffy coloration on the dorsum, sides, and flanks; this is the lightest of all the races and it possesses a long, narrow bill. The light color is most apparent in fresh fall plumage and is rapidly affected by wear and fading, so that birds come to be more ashy in worn plumage; yet this race is still lighter than other races at comparable stages of wear and fading. The flanks are Cartridge Buff with the dorsum slightly darker, more like Cream Buff. The race inyoensis can be distinguished from baileyae by its much paler, buffy, less plumbeous appearance, narrower bill, and longer tail. As compared with abbreviatus it is lighter, less plumbeous on the back with buffy rather than gray flanks, and it has a smaller, narrower bill and longer tail. Inyoensis shares the same bill type with wasatchensis and, as in that race, the flanks and sides are buffier than the back, but the appearance is generally lighter, more buffy, and less greenish. The average tail length is slightly shorter.

Geographic distribution.—Extreme southeastern Oregon, extreme southwestern Idaho, extreme western Utah, Nevada (except northwestern portion), higher mountains of eastern California east and southeast of the Sierra Nevada from the vicinity of the Mono Craters and the White Mountains in Mono County south along the Inyo Mountains to and including the Grapevine, Panamint, and Argus mountains in Inyo County, and Clark Mountain in eastern San Bernardino County.

Specimen localities.—CALIFORNIA: Inyo County: Havaupah Canyon, 7500 feet, Panamint Mts., 2

(May); 3 mi. E Jackass Spring, 6200 feet, Panamint Mts., 13 (Oct.); Roberts Ranch, 8300 feet, Wyman Creek, White Mts., 2 (Aug., Sept.); Silver Canyon, 8000 feet, 7 mi. E Laws, White Mts., 5 (July); White Mts., 21/2 mi. SE of head of Black Canyon, 8000 feet, 2 (July); 5 mi. up Bishop Creek Canyon, 3 (Dec.); Mazourka Cañon, 8000-10,000 feet, 3 (May); E base Waucoba Mt., 7300 feet, 1 (June). San Bernardino County: N side Clark Mt., 7100-7300 feet, 3 (May). Mono County: Benton and vicinity, 5639 to 7500 feet, 16 (June, Sept.); Big Prospector Meadow, 10,300 feet, White Mts., 5 (July); Mono Mills, Mono Lake, 1 (June); 5 mi. E, 1 mi. S Mono Mills, 8300 feet, 4 (June); Pellisier Ranch, 5600 feet, 5 mi. N Benton, 1 (Sept.); McCloud Camp, Cottonwood Creek, White Mts., 3 (July, Aug.). NEVADA: Douglas County: Desert Creek, 6250 feet, Sweetwater Range, 1 (June). Mineral County: N base White Mts., [= Queens Canyon], 111/4 mi. NE Benton Sta., 7200 feet, 2 (Sept.), Esmeralda County: Pinchot Creek, 8200 feet, White Mts., 1 (June); 2½ mi. S Cave Spring, 8000 feet, 1 (June); Chiatovich Creek, 8200 feet, 1 (May). Nye County: N Slope Toquima Mt., 9000 feet, 1 (July); Quinn Canyon Mts., Burned Corral Canyon, 6800 feet, 1 (July); Mohawk R.S., 1 (June); Wisconsin Creek, and vicinity, 8600 feet, 9 (May); 21/2 mi. E, 1 mi. S Grapevine Peak, 6700 feet, 8 (June); 5 mi. W White Rock Spring, 6950 feet, Belted Range, 1 (May). Lander County: Kingston Creek, 8000 feet, 2 (Sept.); 2 mi. E Carroll Summit, 6800 feet, 2 (Aug.); Birch Creek, 7000 feet, 13 (Aug., Sept.); Kingston R.S., 7500-8000 feeet, 21 (June, Sept.); Mahogany Cañon, 7700 feet, 6 (June, Aug.). Clark County: N side Potosi Mts., 7000-8000 feet, 3 (June); Head of Clark Cañon at Sawmill Creek, 8600 feet, Charleston Mts., 1 (June); Lee Cañon, 9000 feet, Charleston Mts., 9 (July, Sept.); Sheep Mts., 6 (Sept.). Lincoln County: Springer Springs, 7000 feet, Mt. Irish, 3 (Sept.). White Pine County: White Pine Mts., 8700 feet, 3 mi. W Hamilton, 1 (Aug.); Lehman Creek, 7500-8000 feet, 10 (May, Sept.); Baker Creek, 7500-9500 feet, Snake Mts., 13 (Sept); Willow Creek, 12 mi. S White Pine County Line, Ruby Mts., 2 (May, June); West side Ruby Lake, 3 mi. S White Pine County Line, 6700 feet, 4 (Oct.); E side Schelbourne Pass, 6800 feet, 1 (Sept.). Elko County: Bear Creek, 8000 feet, Jarbidge Mts., 19 (Sept.); 9 mi. NE Wells, 6000 feet, 9 (Sept.); W side Ruby Lake, 6 mi. N Elko County Line, 1 (Dec.). Humboldt County: Martin Creek, R.S., 7000 feet, Santa Rosa Mts., 20 (June, Sept.). UTAH: Washington County: 3-5 mi. E Pine Valley, 7200-8700 feet, Pine Valley Mts., 14 (June, Sept.). Juab County: S end Deep Creek Mts., 5500 feet, 11 mi. W Trout Creek, near Utah-Nevada border, 5 (May); Queen of Sheba Mine, 8000 feet, W side Deep Creek Mts., 27 (May, June, Sept.); 6 mi. E Indian Village, 8000 feet, Deep Creek Mts., 3 (July). Boxelder County: Pilot Mountain, 1 (July); George Creek, 7500 feeet, Raft River Mts., 5 mi. S Yost, 9 (May); Clear Creek, 7500 feet, N slope Raft River Mts., 5 mi. SW Nafton, 5 (May); One Mile Canyon near Standrod, Raft River Mts., 6 (May, Aug., Sept.). IDAHO: Cassia County: Mt. Harrison, 10 mi. S Albion, 1 (June); Corner Canyon, 4 mi. N Elba, 1 (June). oregon: Malheur County: Rome, Owyhee River, 2 (Oct.).

Geographic variation and intergradation.—Series from central northern Nevada (Santa Rosa, Ruby and Jarbidge mountains) have mighter dorsal coloration than topotypical birds from the Panamint Mountains, Inyo County, California, and have more white on the head, suggesting that this geographical region is the center of differentiation for the race and that the type locality may be somewhat marginal. The bill, however, is slightly smaller in the northern Nevada birds.

The races inyoensis and abbreviatus doubtless blend in southern Oregon, but the area of merging is unknown. A single specimen from Rome, Owyhee River, Malheur County, Oregon, taken October 24 is very pale with buffy flanks, being similar to those from Bear Creek in the Jarbidge Mountains, Nevada, and thus it represents inyoensis. It was referred to grinnelli by Gabrielson and Jewett (1940:434). A December specimen taken not far distant at Ironside, Willow Creek, Malheur River, is darker and grayer on the back and flank, thus being referable to abbreviatus.

Specimens from northwestern Nevada (Pine Forest Mountains, Humboldt County) are closer to abbreviatus as Grinnell (1918:312) noted. He pointed out that the coloration of these birds approaches inyoensis but the tail averages nearly as short as in abbreviatus. The flanks are gray as in abbreviatus.

Another point of contact between *inyoensis* and *abbreviatus* is in the Mono Lake area. Grinnell (1918:512) comments that several examples from along the east flank of the Sierra Nevada in Inyo County insensibly bridge the interval between the two races. Some additional specimens demonstrating this are fall-taken examples from the Benton area, 7000 feet, Mono County, California, and from Bishop Creek Canyon, Inyo County, California. They are grayer and less buffy than *inyoensis* and

thus show intergradation with abbreviatus. In addition to these intermediate forms, one finds from this area of increased variability extremes resembling different races. For instance, an immature male from Pellisier Ranch, 5600 feet, 5 miles north of Benton, taken September 19, 1917, has the bill type of invoensis but resembles gambeli in its rich, brown dorsum. This might be interpreted as an example of extreme foxing except that the flanks are cinnamomeous as in gambeli. This blending of invoensis

Table 6

Measurements of Parus gambeli inyoensis

Dimension	Sex	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	8	188	64.5-75.0	69.41±0.17	2.04	2.93
	9	121	62.3-70.5	66.47±0.17	1.91	2.87
Tail	8	188	54.0-69.4	$61.70 \pm 0.17$	2.32	3.77
	2	120	54.7-66.0	59.69±0.18	2.02	3.38
Bill from	8	182	7.5- 9.2	$8.33 \pm 0.03$	0.42	5.04
nostril	2	116	7.3- 9.3	$8.28 \pm 0.03$	0.41	4.97
Depth of bill	8	165	3.0- 4.2	$3.45 \pm 0.02$	0.33	9.77
	9	108	3.0- 4.0	$3.44 \pm 0.02$	0.21	6.20
Bill width	8	180	2.6- 4.3	$3.63 \pm 0.01$	0.18	5.05
	2	116	3.0- 4.2	$3.60 \pm 0.01$	0.16	4.68
Weight (grams)	8	119	9.5-12.9	$11.18 \pm 0.06$	0.73	6.61
	2	78	9.1-13.2	10.48±0.15	1.42	13.50

and abbreviatus apparently does not occur much farther north than the Mono Lake area, for examples from the Sierra Nevada north of this point are good abbreviatus. It probably does not extend very far to the south either, because there is a barrier between the two races in the nature of the abrupt east face of the Sierra Nevada and the Owens Valley at the base of these mountains.

# Parus gambeli wasatchensis Behle

Parus gambeli wasatchensis Behle (1950:273).

Type locality.—Silver Lake Post Office (Brighton), 9000 feet, head of Big Cottonwood Canyon, Salt Lake County, Utah.

Racial characters and comparisons.—This population is distinguished by dorsal coloration that is intermediate between inyoensis and gambeli. Wasatchensis is closest to inyoensis, showing the same bill type and buffy flank color, but the dorsum is slightly darker, having a greener, less grayish-pink cast; and while the wing lengths are virtually the same, the tail of wasatchensis is slightly longer. Wasatchensis differs from gambeli in having a less brownish dorsum and a longer, more attenuated bill. From grinnelli, wasatchensis may be told by its longer, more tapering bill and lighter dorsum. The greenish cast to the dorsum of wasatchensis shows closer affinity to grinnelli than to gambeli with its brown cast.

Geographic distribution.—Mountains of central and southern Idaho and of Utah, except along extreme eastern and western margins of that state.

Specimen localities.—IDAHO: Valley County: 5 mi. E Warm Lake, 7000 feet, 1 (July); 5 mi. W Cape Horn, Sawtooth Range, 1 (July). Adams County: 3 mi. W Payette Lake, 5400 feet, 3 (July). WYOMING: Uinta County: Fort Bridger, 6700 feet, 1 (Sept.). Utah: Summit County: Smith Morehouse Creek, Weber River, 1 (Oct.). Duchesne County: 4 mi. up Brown Duck Canyon, northwest Moon Lake, 9000 feet, Uinta Mountains, 2 (Sept.). Uintah County: head of Ashley Creek, 9500 feet, near Trout Creek Park, 20 mi. NW Vernal, 6 (Sept.). Davis County: Bountiful Peak Picnic Ground, 8500 feet, head of Farmington Canyon, 1 (Nov.). Tooele County: Stansbury Mountains, 16 (April, July, Aug., Oct., Nov.); Onaqui Mountain, 1 (Nov.); Sheep Rock Mountains, 3 (May, July); Cedar Mountains, 2 (Jan., Sept.). Salt Lake County: Silver Lake P.O. (Brighton), 8750 feet, head of Big Cottonwood Canyon, Wasatch Mountains, 23 (June, Aug., Sept.); Bell's Canyon, 7800 feet, 18 mi. SE Salt Lake City, 1 (Sept.). Garfield County: 1 mi. E Jacobs Reservoir, 10,500 feet, Aquarius Plateau, 10 (June); Boulder, 6200 feet, 1 (July); 5 mi. N Boulder, 7500 feet, SE Base Aquarius Plateau, 1 (June); Kane County: Duck Creek Ranger Station, 8600 feet, 22 mi. SE Cedar City, 12 (June);

Navajo Lake, 9500 feet, 3 (July); Red Canyon, 5700 feet, 6 mi. N Kanab, 4 (Dec.); Tinny Canyon, 5400 feet, 4 mi. NW Kanab, 3 (Sept., Dec.).

Table 7
Measurements of Parus gambeli wasatchensis

Dimension	Sex	Number of specimens	Range	Mean with standard error	Standard deviation	Coefficient of variation
Wing	8	43	67.3-73.3	69.95±0.22	1.49	2.13
	2	33	64.3-69.0	66.41±0.22	1.31	1.97
Tail	8	42	59.0-68.7	$63.18 \pm 0.35$	2.31	3.66
	\$	33	58.0-65.8	60.54±0.30	1.72	2.85
Bill from	8	42	7.9- 9.4	$8.51 \pm 0.09$	0.59	7.01
nostril	2	33	7.3- 9.5	$8.50 \pm 0.07$	0.40	4.74
Depth of bill	3	39	3.0- 4.1	$3.48 \pm 0.04$	0.26	7.61
	2	32	3.2- 4.4	$3.40 \pm 0.48$	0.27	8.12
Bill width	8	41	3.2- 4.4	$3.83 \pm 0.04$	0.25	6.69
	\$	33	3.1- 4.5	3.66±0.05	0.33	9.17
Weight (grams)	8	14	10.3-12.6	11.56±0.17	0.67	5.82
	2	8	9.3-12.0	$10.51 \pm 0.33$	0.95	9.08

Geographic variation and intergradation.—Typical examples of wasatchensis occur in the Wasatch and Uinta mountains of northern Utah and south throughout the mountains and high plateaus of the central part of the state. In surrounding areas this race intergrades with neighboring races. As noted in the account of gambeli, intergradation with that race occurs in northern Arizona and extreme southeastern Utah along the Colorado border as well as in northwestern Wyoming and extreme northeastern Idaho. Intergradation occurs with grinnelli in central Idaho. Specimens from 5 miles east of Warm Lake and 5 miles west of Cape Horn, Sawtooth Range, Valley County, and 3 miles west of Payette Lake, Adams County, are intergrades but are closest to wasatchensis. The race grinnelli, as previously noted, occurs in typical form in Kootenai and Bonner counties. To the west in Utah a cline exists across the eastern part of the Great Basin whereby wasatchensis and invoensis blend from one isolated desert range to the next. This is similar to the gradual blending over a long gradient of grinnelli and abbreviatus in central Oregon and Washington and between abbreviatus and baileyae in the southern Sierra Nevada. Specimens from the Stansbury Mountains are somewhat arbitrarily considered closer to wasatchensis and those from the Deep Creek Mountains are closer to inyoensis. The series from the Pine Valley Mountains in southwestern Utah is referable to invoensis. Specimens from the Raft River Mountains in northwestern Utah could be referred in either direction but I have placed them with inyoensis along with some taken in adjacent Cassia County, Idaho.

# SUBSPECIATION IN Parus gambeli

Within the species at the present time seven geographic races are known, representing different degrees of differentiation. They may be placed in several groups. One group occurs in the Rocky Mountains and is represented by the races gambeli and grinnelli. Members of the "gambeli group" are distinguished by a short, stubby bill type, cinnamomeous color of sides and flanks, long tails, and similar wing-tail ratio even though there are absolute size differences between the two races. In the interior Great Basin and adjacent areas a second group is represented by inyoensis and wasatchensis. This may be termed the "inyoensis group." The members have the same type of long, slender bill, pale buffy color of sides and flanks, and generally pale coloration throughout. The third stock, the "abbreviatus group," ranges through the Cascade-Sierra Nevada Cordillera and detached mountain masses of southern California and northern Lower California and is represented by the races abbreviatus, baileyae, and atratus. Characteristics of this group are a short tail, heavy and moderately long bill type, and prevailing gray coloration. These races differ among themselves primarily in the degree of darkness of gray coloration.

While the races and groups are based on external morphological characters, differences in behavior and ecology probably would be shown to occur if intensive field studies were made. In this connection it is interesting to note that Miller (1934:163) detected a difference in song between representatives of wasatchensis heard at Cedar Breaks National Monument, Utah, and chickadees of the Sierra Nevada region representing abbreviatus or baileyae. He states: "I noted repeatedly that the songs of this chickadee consist of two groups of notes separated by three or more half tones of pitch. In contrast to this type of song are those of the races P. g. baileyae and abbreviatus in which the greatest interval of pitch with rare exceptions is no larger than one whole tone."

The existence of several races of different degrees of differentiation poses questions of whether they have become differentiated in their present environments or have pushed in from other areas and whether they are in process of diverging or merging. Perhaps the well-marked races, gambeli, abbreviatus, atratus, and inyoensis, with their different environments, represent older, stabilized, even parental stocks that have developed in situ in the respective centers of the Rocky Mountains, Cascade-Sierra Cordillera, Sierra San Pedro Mártir, and Great Basin, whereas baileyae, grinnelli and wasatchensis are younger races that are more recently formed as intermediate populations resulting from introgression. Incidentally a conservative view would be to recognize by name only the well-marked races gambeli, abbreviatus, atratus, and inyoensis. This, however, would not reveal the true picture of variation and subspeciation. Grinnelli is situated between gambeli and abbreviatus. While its small size is distinctive and its bill type is that of gambeli, the gray-green dorsal coloration might have arisen from a blending of the brown of gambeli and the gray of abbreviatus. Variation in flank color is erratic, showing in many examples of grinnelli features of one or the other neighboring races. This suggests an origin by introgression. Opposed to this interpretation is the circumstance that the northern Idaho region is a differentiation center for different races of several other species of birds. Wasatchensis similarly is situated between inyoensis and gambeli. The dorsal color tone is intermediate between these races. The bill type, however, is clearly that of inyoensis. The range of abbreviatus covers a very large area, whereas that of baileyae is restricted; and, furthermore, chickadees of this latter race occur in isolated populations on separate mountain ranges. The race bailevae may have arisen from the blending of abbreviatus and a relict atratus stock or it simply may be an intermediate differentiate between the other two races along a step gradient. Atratus may not be a relict stock, for again the San Pedro Mártir region where it exists is a differentiation center. Geographic intergradation has been shown to be present between all neighboring races except baileyae and atratus, between which a geographic hiatus exists. Intergradation occurs between these two races by virtue of individual variation. Regardless of the mode of origin of the several races, the species Parus gambeli is a "plastic" species composed of several populations of subspecific rank. These represent at least two levels of differentiation.

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## FROM FIELD AND STUDY

The Voice and Habitat of the Rufous Nightjar in the Panamá Canal Zone.—The Rufous Nightjar (Caprimulgus rufus) closely resembles the Chuck-will's-widow (C. carolinensis) in pattern and color, but is ruddier, smaller (about 10 inches long), and lacks lateral filaments to the rictal bristles. It occurs through most of tropical South America, extending north into Central America as far as Costa Rica. The Panamá population has been described as the subspecies minimus.

The Ruíous Nightjar is a common bird in the vicinity of Fort Clayton, near the Pacific terminus of the Panamá Canal. In this area it is always found in fairly open country where there are trees and brush along a watercourse or the edge of a lake or pond, and where there are high grasses and weeds nearby. All the birds found at Fort Clayton, with a single exception, were along the course of the Cardenas River, a small stream flowing through the open, hilly part of the reservation. The exception was a bird which was heard calling on three successive nights in April, 1955, from a low tree on the lawn of the Fort Clayton Hospital, which is on a hill about a half mile from the stream. It is perhaps noteworthy that thirty yards from this bird's perch was a large aeration pool on the hospital grounds.

Other areas near Fort Clayton were checked in March and April at the height of the calling season and Rufous Nightjars were found to be common along the upper arms of Miraflores Lake and at several locations on the Canal near the Miraflores Locks. In every instance the birds were found near water in low trees, with open treeless areas and high grass close by. In March several were heard along the Chagres River upstream from the Canal, and one of two birds seen during daylight hours was perched ten feet up on the lower limb of a tree overhanging the edge of a reedy, grassy area about a mile above Gamboa on the Chagres River.

The Rufous Nightjar has a rather toneless but far-carrying call of five notes, the last two from a distance sounding like a single note. The call takes slightly over one second to complete. At close range it is a distinct: Chook! Wick-wick-weé-oh. All notes are approximately of the same low pitch except the last, which drops off slightly. From farther off the call sounds like a whispered: Chuck. Wick-wid-will. The call is similar in pitch but less musical than that of either the Whip-poor-will (C.vocijerus) or the Chuck-will's-widow, and it also differs from the latter in that the initial "chuck" is separated from the remainder of the call by a more definite pause. This initial note is delivered with as much volume as the other notes and is always heard.

In the Panamá Canal Zone the Rufous Nightjar calls mostly during the dry season, which here usually lasts from January to April or early May; it is almost never heard during the rainy season. In 1953 and 1954 no specific effort was made to record the calling habits of this bird, although my notes indicate that I first heard the call in 1953 on February 19 and in 1954 on February 23. In 1955, however, an accurate record was kept of its calling habits at Fort Clayton. The first call was noted on the early evening of February 3, one bird calling intermittently for a period of 45 minutes. From that date on they were heard almost every night until the middle of May when the rains started again. Calling was at its height during the month of April, which that year was very dry in Panamá, with trade winds blowing during the days and the nights usually being calm and clear. During that period from my house at Fort Clayton I could usually hear three to six birds calling, starting shortly after sundown and continuing throughout the night. The earliest calls would commence at 7:00 p.m. and the latest morning call noted was at 5:30 a.m., shortly before dawn. I have never heard the Rufous Nightjar call during daylight hours.

In 1955 the first rains of the season at Fort Clayton fell on May 9. For a week thereafter the weather was overcast, very hot, and humid, although the regular rainy season pattern of almost daily downpours did not set in until May 20. On May 8, as for the month preceding, several Rufous Nightjars were heard calling throughout the night. On May 9, after the first heavy rain, no birds were heard until 9:45 p.m., when a single bird called for three minutes and then stopped. The following night a bird called for 20 minutes starting at 10:30 p.m., then stopped for an hour when it resumed calling and continued intermittently until midnight. Single birds were heard for a few minutes at a time on the nights of May 11, 12, and 13, and then none until June 7, when one bird was heard calling a few times about one-half hour before dawn. No calls, were heard after that date.

It was noted that un different nights and even at different times of the same night the rate of calling varied considerably for individual birds. On some nights all birds heard were calling faster than usual. The slowest individual heard called at a rate of 16 repetitions per minute and the fastest at a rate of 41 per minute. Of all the birds timed, the average rate of calling was 28 per minute.

The following table gives the calling rates of four Rufous Nightjars for a ten-day period in April, 1955. Slight differences in their calls, as well as the fact that individuals habitually used the same tree for a calling perch, made it fairly easy to distinguish these four birds, even when all were calling at the same time. Their perches were spaced about 200 yards apart along the course of the Cardenas River near my house. They were timed for periods of five minutes or more beginning at each of the hours indicated. On the two evenings when the very fast rates are recorded my notes show that the weather was extremely hot and humid, much more so than usual.

Calling Rates of Rufous Nightjars

Date in			Number of ca	lls per minute	
April, 1955	Hour	Bird A	Bird B	Bird C	Bird D
18	12:01 a.m.	29	24	20	***
18	4:00 a.m.	30	26	20	24
19	12:00 mid.	29	24	19	23
23	3:45 a.m.	25	18	18	20
24	9:00 p.m.	29	24	24	20
24	12:00 mid.	30	26	24	23
25	7:30 p.m.	28	24	22	***
26	1:00 a.m.	29	24	19	24
26	9:00 p.m.	30	24	26	****
28	7:45 p.m.	41	30	32	25
28	10:15 p.m.	32	28	26	****
30	7:30 p.m.	40	39	30	****
30	11:00 p.m.	29	25	22	24

During the month of April, when calling was at its height, individuals would call continuously for periods of five minutes to an hour or more. Often one would stop for a few minutes only to resume calling, keeping this up for several hours. On April 19, 1955, I recorded a remarkable series of calls for one Rufous Nightjar whose perch was a low tree on the river bank about 300 yards from my house at Fort Clayton (Bird A of the table). This individual had been heard at intervals earlier in the evening, but at fifteen minutes past midnight it began a session of continuous calling that went on without a break until 4:27 a.m., a total of 252 minutes! The rate of calling was nearly constant; I checked it at intervals of about fifteen minutes and it varied but little from a steady 29 calls per minute. It is believed that this record of over 7000 consecutive calls is the longest ever noted for a goatsucker. Sprunt (Florida Bird Life, 1954:258) mentions a count of 834 consecutive calls for the Chuck-will's-widow and Cleaves reports over a thousand consecutive calls for the Whip-poor-will (Mulaik, Lee, and Stillwell, Auk, 70, 1953:368).

Several birds were observed while calling. The beam of a powerful flashlight did not seem to disturb them m great deal and it was possible to approach to within m few yards before they would stop calling and fly off. Every bird seen calling was perched crosswise on m bare limb, usually on the end, under m canopy of overhanging branches. When calling the mouth is opened widely and the whole body vibrates with the effort of the call. Two birds observed during the day were perched lengthwise on limbs, in the manner of other goatsuckers. No birds were ever seen on the ground, although the Pauraque (Nyctidromus albicollis), which in this area frequents the same habitat as the Rufous Nightjar, was always found on the ground.—F. O. Chapelle, Medical Field Service School, Fort Sam Houston, Texas, September 24, 1955.

Scissor-tailed Flycatcher in Idaho.—While vacationing along the Wood River, Idaho, fifteen miles from Sun Valley and at 6800 feet elevation, my husband and I saw a Scissor-tailed Flycatcher (Muscivora forficata). It was observed on August 6, 7 and 16. It was a female or immature, since the

tail was not as long as in adult males, but the tail was definitely forked. The head, breast and back appeared almost white as it sat on top of small pines, three to five feet high usually, and this was what first attracted our attention to it. When it flew, the salmon-pink wing linings showed plainly and there was a pink wash on its sides. The red patch also showed on the wing in flight.

The air was full of flying Violet-green Swallows the first time we saw the flycatcher and each time it would take wing the swallows would dart at it. Apparently they recognized it as a strange bird and indeed it was far out of its range.—FLORENCE THORNBURG, Tucson, Arizona, September 9, 1955.



Fig. 1. Nest and young of Striped Horned Owl in Panamá

A Nest of the Striped Horned Owl.—On January 8, 1953, two young Striped Horned Owls (Rhinoptynx clamator) were discovered on their nest in a citrus orchard at Juan Mina Station located on an island in the Chagres River, Panamá. The young, not more than a few weeks old, are pictured (fig. 1) on the nest which was merely a beaten place in the grass on the ground. A female bird, apparently the mother, had been collected the day before.—Frank A. Hartman, Ohio State University, Columbus, Ohio, September 24, 1955.

The Western Grebe Taken on Hook and Line.—Over a period of two years at the United States Naval Receiving Station, Seattle, Washington, the writer had many opportunities to observe the occurrence, relative abundance, and feeding habits of the Western Grebe (Aechmophorus occidentalis) and it was noted that this bird's habits are remarkably influenced in the pier areas by the large ships at berth. Ordinarily the anchor lights of ships are turned on at night and directed at the water's surface. These lights attract fish of many species, chief among which are the starry flounder (Platichthys stellatus), various sculpins, sable fish (Anoplopoma fimbria), rock cod or rock fish (Sebastodes sp.), rarely a thread eel (Nemichthys avocetta), and many small fishes including the herring (Clupea pallasii).

The Western Grebe was observed in flocks of various sizes at all times of the night and early morning actively engaged in diving for the smaller fish in the areas flooded by the ships' lights. Dr. Philip Westling of Zillah, Washington, and the writer frequently fished in these light-flooded areas for the young king salmon or "blackmouths" common in Elliott Bay. This fishing was done at all hours of the night and early morning, using spinning tackle baited with a whole or diagonally "plugged" herring on a double "set-up" hook commonly employed in salmon sports fishing. On four different occasions while retrieving casts, Western Grebes were hooked. Our estimate of the depth in each instance was 15 to 20 feet. The hooked birds surfaced and tried to fly, but being securely hooked, they had to be brought in.

In each instance when the hooked bird surfaced, it cried out repeatedly and struggled violently to escape. The rest of the birds of this species in the area invariably crowded around the stricken bird as if to try to help it. All four of the birds were hooked securely in the side of the mouth. Some difficulty was encountered in dislodging the hooks because of the pugnacity of the birds and their repeated attempts to bite us. All birds were returned apparently unharmed to Elliott Bay. One grebe regurgitated two partially digested candlefish (Thaleichthys pacificus) while being unhooked.

The taking of the Western Grebe in the manner described at midnight, 2 a.m., 3:30 a.m., and 4:50 a.m. suggests that either this bird feeds at night to quite a degree or that the berthed ships in the Seattle waterfront area are providing a unique feeding opportunity of which a limited number of birds have taken advantage.

This bird adds another to the list of those taken on hook and line by the writer while sports fishing in the western United States. The others so taken include the Nighthawk (Chordeiles minor), the California Gull (Larus californicus), and the Water Ouzel (Cinclus mexicanus). Both the Water Ouzel and the Nighthawk were taken on small dry flies on Diamond Fork Creek, Utah County, Utah.—S. Larry Chatwin, Division of Biology, University of Utah, Salt Lake City, Utah, October 25, 1955.

Pileated Woodpecker South of the Sierra Nevada in California.—On September 12, 1952, a pair of Pileated Woodpeckers (Dryocopus pileatus) was seen near the Breckenridge Mountain Camp Ground, 6500 feet, Kern County, California. The birds were present in the same area on the following day. Grinnell and Miller (Pac. Coast Avif. No. 27, 1944:230) reported Pileated Woodpeckers from the Greenhorn Mountains just north of the Kern River Valley in the extreme southern Sierra Nevada. I am not aware of records south of this valley other than the one here reported.

The habitat appeared suitable for these birds in that it was an old forest composed of yellow pine, Douglas fir, sugar pine and large black oaks. On a short visit to this same area the following spring I was unable to locate these woodpeckers. They may not be resident in this locality.—Wade Fox, Jr., Louisiana State University, School of Medicine, New Orleans, Louisiana, October 31, 1955.

Galapagos Penguin in Panamá.—Recently while in Panamá I learned that a penguin had been captured alive on the Pacific coast in February, 1955, and that the skin was in the Museo Nacional de Panamá. The director of that museum, Dr. Alejandro Méndez Pereira, kindly lent me the specimen to enable comparison with specimens in the American Museum of Natural History. The penguin is an immature Galapagos Penguin (Spheniscus mendiculus), hitherto recorded only from the Galapagos Islands. Identification was confirmed by Robert Cushman Murphy and Dean Amadon. In color the Panamá bird closely resembles three immature examples in the American Museum from the Rothschild Collection, taken on November 11, 1897, by R. H. Beck at Tagus Cove, Albemarle Island, Galapagos Archipelago. In any plumage S. mendiculus differs from its congeners by its small size and by relatively longer and more slender bill. The specimen measures: wing, 145 mm.; culmen, 58 mm.; bill from gape, 66 mm.; front of nostril to tip of bill, 30 mm.; vertical depth of bill at base, 18 mm.; foot (from heel to tip of claw of middle toe), 88 mm.

To Dr. Méndez Pereira I am indebted for the following information: The penguin was taken at Puerto Armuelles, province of Chiriquí, in the middle of February, 1955, by a swimmer, who reported that it was accompanied by a larger individual, which avoided capture. The bird was purchased by Sr. Guillermo Tribaldos of David, Chiriquí, who kept it there in a river in a large wire mesh cage

so placed that the current would bring fresh and living food through the wide mesh. The penguin survived for a month and a half.

There appears to be no prior record of a penguin taken in Middle America. Yet Mr. James Price of Panamá assures me that some years ago he was offered several unidentified penguins captured alive on the Pacific coast of Panamá. Hence this may not be an isolated incident.

According to Murphy (Oceanic Birds of South America, 1, 1936:466 ff.) the Galapagos Penguin is known only from the Galapagos Archipelago, particularly the central and westerly islands lying on or just below the Equator; it feeds in the cool waters of the Humboldt Current, which wash the shores of these islands. Murphy mentions (loc. cit.) that it has been "doubtfully reported from Wenman Island," which is isolated and lies at latitude 1° 20' N, to the northwest of the main Galapagos Archipelago. The Galapagos extend east to longitude 89° 16' W; Puerto Armuelles lies at about longitude 82° 50' W and latitude 8° 15' N-some seven hundred miles to the northeast. Since the Humboldt Current in its course through the Galapagos flows toward the west, it is a matter of speculation how a non-migratory and non-volant penguin from these islands ranged so far to the northeast. However, a short distance north of the Galapagos Archipelago, another current, the Equatorial Countercurrent, flows toward the east, veering northward as it approaches the continent. In some years, during the early months, this countercurrent displaces, or partly displaces, the Humboldt Current about the Galapagos. It is possible that a penguin chancing to stray into the countercurrent might reach the coast of Panamá. Perhaps a stronger possibility is that fishermen or yachtsmen may have captured the bird and later allowed it to escape near Panamá waters.—Eugene Eisenmann, New York City, New York, September 29, 1955.

White-throated Sparrow in Humboldt County, California.—On September 27, 1955, we observed a White-throated Sparrow (*Zonotrichia albicollis*) at close range in a thimbleberry and salal thicket at the west end of the Wildlife Building on the Humboldt State College Campus, Arcata, California. There are few records for this area, although the species has been recorded in Eureka in the months of November, March, and May and at Adams, Del Norte County, on November 4 (Grinnell and Miller, Pac. Coast Avif. No. 27, 1944:526).

This record is of significance because of the early date for the area.—Charles F. Yocom and Rolf E. Mall, Humboldt State College, Arcata, California, October 15, 1955.

Distributional Data on the Birds of the White Mountains of California and Nevada.—The White Mountains are the largest and highest of the mountain ranges constituting the Great Basin mountain province of California. The breeding birds of the boreal areas of this province were tabulated in 1951 (Miller, Univ. Calif. Publ. Zool., 50, 1951:584–591) from a scattered literature and from the notebook records of field parties of the Museum of Vertebrate Zoology which have operated in the White Mountains, chiefly in 1917. When this tabulation was prepared, certain doubts remained about the summer resident status of some species and as a consequence a field party visited the mountains under the leadership of Russell in May and June of 1954 in order to gain further information. In addition to Russell, Francis S. Williamson, Joseph G. Hall, A. Starker Leopold, Robert S. Hoffmann and Jerry Russell took part, the last three only in the last week of June. Parts of the range lying in Esmeralda County, Nevada, were visited, as well as those in Mono and Inyo counties, California. The following data supplement the previous records for this mountain system.

Dendragapus fuliginosus sierrae. Sooty Grouse. No specimens of this type of grouse from the White Mountains were extant previously, although the species was known to occur. In 1944 Grinnell and Miller (Pac. Coast Avif. No. 27:115–116) tentatively included the population of these mountains in D. f. howardi. Russell took three males and one female in May, 1954, in Trail Canyon, 8900 feet, Esmeralda County, Nevada, and an adult female and downy young at 8200 feet on Wyman Creek, Inyo County, on June 6 and 7. The backs of the males as a group are intermediate in color and pattern between those of sierrae and howardi in the same way that grouse of the Yosemite district and the Sweetwater Mountains of northern Mono County are intermediate. The tails of adults are intermediate in length although closer to sierrae than to typical howardi: § \$, 173, 174, 183; \$ \mathbb{Q}, 147,

148 mm. The specimens are, then, best placed with sierrae, as are those of the Yosemite district, rather than with the howardi-like birds of the Kearsarge area of the Sierra Nevada of west-central Inyo County. The multiple hooting from trees and the orange color of the neck air sacs normal for the coastal forms of Dendragapus were noted.

Asio wilsonianus. Long-eared Owl. This is not normally a boreal zone species, but it is worth noting that in the White Mountains it ranges up to 9500 feet where on June 20 large young were seen on Cottonwood Creek. Mono County.

Aegolius acadicus acadicus. Saw-whet Owl. Although this owl is known from other mountains in the Inyo area, it has not been recorded breeding in the White Mountains. Juveniles were taken on Indian Creek at 7400 feet, Esmeralda County, on June 1 and 2 and on Wyman Creek at 8200 feet, Inyo County, on June 8, 9, and 13.

Chordeiles minor hesperis. Booming Nighthawk. Two males were taken on Wyman Creek at 6750 feet, Inyo County, on June 16; testis length 7 mm.

Stellula calliope. Calliope Hummingbird. This species probably breeds although actual nesting has not yet been observed. A female taken on June 12 at 8200 feet on Wyman Creek, Inyo County, had ova up to 1 mm. in diameter.

Sphyrapicus varius nuchalis. Yellow-bellied Sapsucker. The Great Basin race nuchalis proved common in the aspens and willows of Cottonwood Creek, Mono County, at 9500 feet. Sapsuckers were seen feeding young on June 19 and 28. Among the eight birds taken there was no sign of characteristics of S. v. daggetti of the Sierra Nevada.

Empidonax difficilis difficilis. Western Flycatcher. A male in breeding condition (testis 6 mm.) was taken on June 27 at 9500 feet on Cottonwood Creek, Mono County.

Nuttallornis borealis. Olive-sided Flycatcher. Although some reservation was expressed earlier (Grinnell and Miller, op. cit.: 263) about the breeding of this species in the White Mountains, there can now be no doubt. Birds in song and full breeding condition were taken as late as June 22 on Cottonwood Creek.

Sitta canadensis. Red-breasted Nuthatch. Apparently summer resident in small numbers. A male in breeding condition was taken in Trail Canyon, Esmeralda County, on May 26 and others in worn adult plumage and post-breeding condition were taken on June 22, 27, and 29 in the Cottonwood Creek area at 9500 feet, Mono County.

Sitta pygmaea melanotis. Pigmy Nuthatch. Contrary to expectation, this nuthatch proved to be nesting in the bristle-cone pines in the Cottonwood Creek area, 9500 to 10,500 feet, Mono County. Nests with young were found on June 21, 23, and 27.

Myadestes townsendi townsendi. Townsend Solitaire. Although this species is known to nest in the Panamint Mountains, it has not been reported breeding in the White Mountains. A laying female was taken on June 28, at 9500 feet on Cottonwood Creek, Mono County.

Regulus satrapa olivaceus. Golden-crowned Kinglet. A male in breeding condition (testis 5 mm.) was taken on May 26 in Trail Canyon, Esmeralda County, at 8900 feet in limber pines. Probably the species nests in small numbers in the better stands of conifers in the range.

Regulus calendula cineraceus. Ruby-crowned Kinglet. This species breeds commonly. One was found building a nest in a lodgepole pine 8 feet above ground on Cabin Creek, Mono County, at 10,500 feet on June 4.

Vermivora pinus. Blue-winged Warbler. A vagrant of this eastern species was detected by Russell on Wyman Creek, Inyo County, at 7000 feet in willows, on June 16. It proved to be a male with the testes 4 mm. in length. This is the first record of this species west of the Great Plains.

Vermivora virginiae. Virginia Warbler. Although this warbler previously was reported as rare in these mountains, it proved to be fairly common in mountain mahogany habitat. In the Cottonwood Creek basin at 9500 feet, Mono County, seven breeding males were taken. A female with a brood patch was taken on Wyman Creek, Inyo County, on June 16.

Oporornis tolmici tolmici. Tolmic Warbler. A high-altitude breeding area for this species was at 9500 feet on Cottonwood Creek.

Geothlypis trichas occidentalis. Yellow-throat. An exceptionally high breeding station was represented by a singing male (testis 7 mm.) taken on June 7 on Wyman Creek at 6700 feet.

Loxia curvirostra grinnelli. Red Crossbill. Family groups containing streaked juveniles were taken

on Indian Creek at 7400 feet, Esmeralda County, on May 31 and June 1, and on Wyman Creek, Inyo County, at 6750 to 8200 feet on June 12 and 15. Similar occurrences were previously known for the Grapevine Mountains to the southeast.

Junco caniceps caniceps. Gray-headed Junco. This form of junco was unexpectedly well represented and several were taken that lacked any hybrid features involving Junco oreganus thurberi. The latter was of course common. A considerable introgression of the two types is taking place here which may more appropriately be analyzed later when additional data are obtained.

The results of the further exploration of the White Mountains here reported add seven boreal species as probable or certain summer residents of the Great Basin mountain province of California that also occur in the Sierra Nevada. This has the effect of reducing the faunal difference score (see Miller, 1951, op. cit.:587-588) between the two boreal areas from 51 to 44. This alteration in value still leaves the Great Basin mountain province of California highly distinct from related provinces to the west and the comments offered earlier (op. cit.) concerning this situation are still appropriate.

—ALDEN H. MILLER, and WARD C. RUSSELL, Museum of Vertebrate Zoology, Berkeley, California, September 9, 1955.

Observations on Red Crossbills in Marin County, California.—In the spring and early summer of 1954, Red Crossbills (*Loxia curvirostra*) were observed approximately two miles northwest of Inverness, Marin County, California. The area, known as Inverness Ridge, is covered predominantly with Bishop Pine (*Pinus muricata*) and is about 600 feet above sea level. The birds were first seen on March 15 when a flock of at least five individuals was flushed from several points on the ridge. Other dates of occurrence and numbers seen were as follows: April 11, 5; April 20–24, 6; April 29, flock; May 2, flock; May 13–14, 18; May 16, 25; May 22, flock; May 31, 40; June 11, 30. From these records it would appear that the number of individuals on the ridge increased as the season progressed.

While feeding, the crossbills were quiet as usual and difficult to locate and observe, but on three occasions we were able to watch their foraging activities. At no time were they seen foraging on ovulate cones but always on or near staminate cones toward the tops of the trees. Indeed, several of the birds that were collected had their bills covered with pollen. The stomach contents of nine birds consisted of minute insect remains, insect eggs, and grit. From the mouth and esophagus of four birds were taken numerous larvae of a sawfly, Xyela sp. (Hymenoptera: Tenthredinidae). This identification was made by Dr. B. D. Burks, Entomology Research Branch, United States Department of Agriculture, Washington, D. C.

Nine specimens were collected, four on May 31 and five on June 11. The testes of six males ranged from 2.0 to 4.0 mm. in length and follicles in the ovaries of the three females included were in no instance greater than 1 mm., indicating that the crossbills were not breeding in this locality. Males averaged 41.2 gm. in weight; females, 37.5. All were adults on the basis of skull ossification and showed varying amounts of fat. There was no noticeable molt among any of the specimens except for two males that were molting a few crown feathers. The specimens have been identified as L. c. grinnelli by Alden H. Miller and have been deposited as skins in the Museum of Vertebrate Zoology.

There are three previous records of this species at Nicasio, Marin County: specimens of the race sitkensis taken on October 28, 1878, and on February 21, 1909, and specimens of grinnelli taken on March 5, 1895.—David W. Johnston, Department of Biology, Mercer University, Macon, Georgia, and Robert A. Norris, Aiken, South Carolina, September 16, 1955.

Eggs of the California Quail in the Nest of a Spotted Towhee.—On April 22, 1950, near Eagle Rock, California, Elvirita Bleitz, Loren Whitelock, Henry Isham and I found the nest of a Spotted Towhee (*Pipilo maculatus*) on the ground in a tangle of wild raspberry bushes. The nest contained four young about three days old and two unhatched eggs of the California Quail (*Lophortyx californicus*). The eggs were fertile and well incubated. On April 28 I returned and found that a riding horse had died nearby and that in the disturbance of hauling it away the nest had been de-

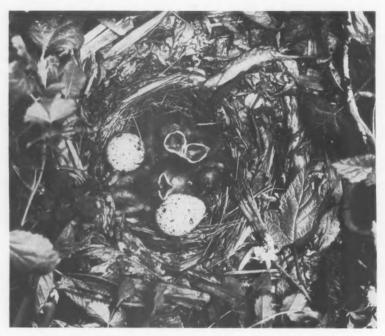


Fig. 1. Nest and young of Spotted Towhee with eggs of the California Quail.

stroyed. I found one of the quail eggs nearby which had been broken. It contained a chick nearly ready to hatch.

Bent (U.S. Nat. Mus. Bull. 162, 1932:63) gives several instances of the California Quail laying eggs in nests of other species.—Don Bleitz, Los Angeles, California, July 15, 1955.

Additional Data on the Birds of Guadalupe Island.—In our recent paper on the birds of Guadalupe Island, México (Condor, 56, 1954:283-294) the following errors and omissions in the check-list and bibliography were made and require correction. The Eared Grebe (Colymbus caspicus californicus) should be included as an accidental visitor as a specimen was reported by Rothschild and Hartert (Novit. Zool., 9, 1902:416). The year of the last record for the Guadalupe Petrel (Ocean-odroma macrodactyla) is not 1919 but 1912, as reported by Davidson (Condor, 30, 1928:355-56). We are indebted to Dr. Alexander Wetmore for calling this lapsus to our attention. In addition to Mrs. Davidson's paper, that of Bond and de Schauensee (Acad. Nat. Sci. Phila. Mono., 6, 1944:7-56) should have been included in the list of pertinent references published since 1927. The latter work mentions several specimens collected at Guadalupe Island, including the second island record for the Osprey (Pandion haliaëtus carolinensis), which should therefore be considered a casual rather than an accidental visitor according to our use of the terms.—Thomas R. Howell and Tom J. Cade, Department of Zoology, University of California, Los Angeles, California, September 22, 1955.

## NOTES AND NEWS

Dates for the Annual Meeting of the Cooper Ornithological Society in Seattle in June of this year have been changed to the 15th, 16th, and 17th, Friday to Sunday. These earlier dates were necessitated by corresponding changes in the meeting time of the Pacific Division of the American Association for the Advancement of Science.

The Assistant Editors of The Condor, Richard F. Johnston and Robert K. Selander, leave the editorial headquarters of the journal in the spring semester of this year to take new academic positions at New Mexico College of Agriculture and Mechanic Arts and the University of Texas, respectively. Their assistance in the editing of The Condor will be sorely missed, and the senior editors take this occasion to express heartfelt thanks to them for the extensive and skillful aid they have given.—A.H.M.

The Frank M. Chapman Fund was established to provide financial assistance to individuals conducting research in any branch of ornithology. The awards are usually made to younger scientists, in particular graduate students, but there are no hard and fast restrictions. Applicants should bear in mind that the field stations operated by the American Museum of Natural History are frequently suitable and available for ornithological as well as other types of scientific work. The Archbold Biological Station at Lake Placid, Florida, the Southwestern Biological Station in the Chiricahua Mountains of Arizona, and the Lerner Marine Station at Bimini, British West Indies, as well as the collections and laboratories of the Museum itself should be mentioned in this connection. When research sponsored by the Chapman Memorial Fund involves collecting, it is expected that, after completion of the study, a representative series of specimens will be contributed to the collection of the Museum. A copy of any published results of work supported in whole or in part by this Fund should be submitted for the record and will, it is hoped, give credit to the Fund for the aid received.

Annual awards are made from the Chapman Fund during the month of April. Applications should be received before March 31 of the year in question. Each applicant should state clearly the nature of the proposed research and give a careful estimate of the financial requirements of the project. Letters of recommendation should, whenever possible, be included. All correspondence should be directed to the Chairman, Chapman Memorial Fund Committee, Department of Birds, American Museum of Natural History, Central Park West at 79th Street, New York 24, New York. The present members of the Committee are Dean Amadon, Walter W. Naumburg, Albert E. Parr, George Gaylord Simpson, and John T. Zimmer, Chairman.

### COOPER SOCIETY MEETINGS

#### NORTHERN DIVISION

OCTOBER.—The monthly meeting of the Northern Division of the Cooper Ornithological Society was held on October 6, 1955, at the University of California, Berkeley. The following names were proposed for membership: George E. Lippert, Brown Road Albion, N.Y., and John M. Burns, Museum of Vertebrate Zoology, University of California, Berkeley 4, Calif., by R. K. Selander; and Mrs. Harriet Pauline Thomas, 32 Stoddard Way, Berkeley 8, Calif., by Junea W. Kellv.

Eric Reynolds described conflicts between the human population and several bird species on Midway Island, which he visited during the summer. Howard Cogswell reported a probable Ashy Petrel at Bay Farm Island on September 23.

Alden H. Miller of the Museum of Vertebrate Zoology spoke on the "Birds of Mountaintop Islands in Nevada and California" and illustrated his talk with colored photographs.—RALPH J. RAITT, Secretary.

NOVEMBER.—The regular meeting of the Northern Division of the Cooper Ornithological Society was held on November 3, 1955, at the University of California, Berkeley. Mr. Robert Galati, 345 Leicester Ave., Duluth, Minn., was proposed for membership by C. V. Duff.

Howard Cogswell presented an oral communication in the form of a request for members in the Oakland area to watch for and count Robins flying at sunset toward Joaquin Miller Park where there is a roosting site used by an estimated minimum of 20,000 Robins. The speaker of the evening was Edward S. Ross of the California Academy of Sciences. His topic was "A Naturalist in the Andes"; the lecture was well illustrated by colored slides.—RALPH J. RAITT, Secretary.

#### SOUTHERN DIVISION

OCTOBER.—The monthly meeting of the Southern Division of the Cooper Ornithological Society was held on October 25, 1955, at the Los Angeles County Museum. The following were proposed for membership: Morgan Monroe, 2802 N. 21st St., Phoenix, Ariz., and Charlotte L. O'Keefe, 4768 West 6th Ave., Vancouver 8, B.C., by Jack C. von Bloeker, Jr.; and Jean M. Wright, 714 S. Crescent Ave., Cincinnati 29, Ohio, by C. V. Duff

Ed N. Harrison announced the death of Dr. Stanley G. Jewett, whereupon a resolution of sympathy was passed and the secretary instructed to send Mrs. Jewett a letter of condolence.

Field observations were given as follows: Sidney Peyton announced that the Fish and Wildlife Service in checking salmon in the Copper River area in Alaska found Trumpeter Swans nesting this year and that 50 adults and several cygnets had been seen. On October 1 and 2 R. Dudley Ross saw two Great Gray Owls at Yosemite. In addition, he reported the return of a Virginia Warbler to the home of Helen Pratt in Eagle Rock for the second consecutive year. The bird was present on September 20 and continued to the date of the meeting. Arnold Small noted an immature Franklin Gull and three Knots on Newport Bay on October 2 and 16. Dorothy Groner, Sidney Peyton and others reported seeing five California Condors back of Fillmore on October 16, and also one Clark Nutcracker at about 4000

The subject of the speaker, Cornelius G. Willis, was "Candid Camera Studies of California Birds."

—DOROTHY E. GRONER, Secretary.

For Sale, Exchange, and Want Column—Each member of the Cooper Society is entitled to one short advertising notice in any issue of the Condor free. Notices of over 3 lines will be charged for at the rate of 25 cents per line. Send advertising copy to Jack C. von Bloeker, Jr., Los Angeles City College, 855 N. Vermont Ave., Los Angeles 29, California.

FOR SALE—The Emu, vols. 4-50, inclusive, except part 4, vol. 8. Three volumes cloth-bound, remainder in parts, as issued; a rare series in excellent order.—Ken L. S. Harley, 30 Gresham St., East Brisbane, S.E. 1, Queensland, Australia.

Wanted—Florence M. Bailey, "Among the Birds in the Grand Canyon Country," National Park Service, 1939, 211 pp. Please state price and condition.—Milton C. Moore, 501 Lincoln Ave., N.W., Apt. 3, Canton 8, Ohio.

Wanted—Journal of Mammalogy, unbound numbers, all of volume 5 (1924), number 3 of volume 13 (1932), and number 4 of volume 1 (1919); please quote prices.—Ward C. Russell, Museum of Vertebrate Zoology, University of California, Berkeley 4, California.

For Sale—Condor, volumes 10-52 (1908-1950), unbound; Auk, volumes 19-64 (1902-47), unbound; also Ridgway's Birds of North and Middle America, parts 1-8; and Bent's Life Histories of North American Birds, various volumes, including all early ones; any reasonable offer will be gladly considered.—ALLAN C. Brooks, *Pender Island, British Columbia*.

# PRICE LIST OF PUBLICATIONS ISSUED BY THE COOPER ORNITHOLOGICAL SOCIETY

## January 1, 1956

In issuing this new list we have made many changes but have endeavored to price the items as low as is consistent with our limited editions and in accordance with a recent inventory. Many of our publications are now nearly depleted and some entirely sold out. All these publications are sent post paid anywhere in the United States; for sales in California please add 3% sales tax on all items except the Condor journal.

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